Movement patterns of the European lobster *Homarus gammarus*: investigating the effects of habitat use and behaviour patterns on catchability

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Abstract

Catch per unit effort (CPUE) is an index of abundance used in fisheries stock assessments. CPUE is typically calculated using fishery data and standardised using statistical methods. A major assumption of fisheries stock assessments is that all individuals are equally available to the fishery, neglecting the possibility that individual-level variability in physical traits, internal states, and expressed behaviour will likely change over time, affecting the probability of capture. However, many knowledge gaps exist regarding behaviour of free-ranging species. This study used fine-scale acoustic telemetry data to quantify free-ranging behaviour of the commercially important European lobster to improve uncertainty surrounding estimates of catch. Behaviour in the vicinity of traps was quantified using an experimental approach that highlighted the highly variable response rate at which lobsters approach traps, and the importance of field studies to capture the full range of movements when compared to mesocosm studies. The interaction between animals at traps is an important aspect of catch, but space-sharing and interaction between free-ranging lobsters has not previously been quantified. A hierarchical approach was used to assess space-sharing, contact rates, and fine-scale interaction between lobsters of the same, and opposite sex. Some lobsters interacted with multiple individuals, commonly on shelter providing substrate; space-sharing and interaction was likely driven by more mobile males. Trap exposure has previously been correlated with increased movement, but the fine-scale drivers of movement, and behavioural states relating to movement, have not been identified. Different aspects of lobster movement were investigated and drivers of movement varied by individual. Interpretation of results varied with the sampling period highlighting the importance of correctly matching the resolution of the behaviour to that of the data collection. Finally an individual-based model was used to demonstrate how movement and behaviour of lobsters can affect catch, to allow better informed sustainable management practices.

Dedication

This thesis is dedicated to my family who instilled in me from a young age the importance of a curious mind and an appreciation of the natural world.

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Declaration

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The data used in Chapters 3 and 4 were collected by Dr. Skerritt during his PhD: Skerritt, D. J. (2014). Abundance, interaction and movement in a European lobster stock. Newcastle University.

All other work was done by Kirsty J. Lees.

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Chapter 1. Introduction

1.1 Background

Movement is a fundamental aspect of many species life cycles; it can be of both ecological and commercial importance, and has been the focus of much research (Holyoak et al., 2008). Individual movement patterns can impact monitoring protocols by affecting individual detectability (Bailey et al., 2004; Stewart et al., 2018; Heupel et al., 2006). Management strategies of mobile resources should consider the possible role of movement in connecting local populations (Morales et al., 2010), its impact on population estimates (Horton and Letcher, 2008), and how movement might influence the effectiveness of designated protected areas (Grüss et al., 2011b,a). Movement can take the form of self-propelled locomotion, or passive transport by physical processes (Gilg and Hilbish, 2003), with many species utilising a number of different habitat types throughout their life. For example, the life cycle of many non-mammalian marine organisms includes a passive planktonic stage followed by a later phase of self-propelled movement (Pechenik, 1999). Movement has evolved through a number of biologically important processes including density-dependence (Laurel et al., 2004), inbreeding avoidance (Cowen and Sponaugle, 2009), habitat suitability (Van Dyck and Baguette, 2005), and physiological constraints (Durban and Pitman, 2012); the understanding of these drivers is central to the sustainable management of many species.

In recent years improved technology and miniaturisation has lead to an increase in animal tracking, or bio-logging, resulting in near continuous tracking of individuals and ever increasing large and complex datasets of animal movement (Nathan et al., 2008; Tomkiewicz et al., 2010). However, there remains a lack of information on the movement and home-range size of many commercially important marine species, often due to cryptic behaviours, such as those exhibited by some crustacean species, and by the added complexity of marine-based tracking that has traditionally lagged behind terrestrial technologies (Pittman and McAlpine, 2003; Hussey et al., 2015). The continued development of acoustic telemetry (Hockersmith and Beeman, 2012) means that fine-scale, spatially precise locations can be achieved and acoustic telemetry is now widely utilised across taxa providing an effective tool to address knowledge gaps associated with fisheries management (Hussey et al., 2015; Crossin et al., 2017).

The European lobster *H. gammarus* is a commercially important high value crustacean throughout its eastern Atlantic range (Triantafyllidis et al., 2005). United Kingdom landings of *H. gammarus* are currently responsible for 12 % of the value of all UK shellfish landings (£12 $^{-}$kg), despite only contributing 2 % of the total landings (Marine Management Organisation, 2017). *H. gammarus* is one of only two species within the *Homarus* genus. Much research has focussed on the closely related *H. americanus* in response to historic declines, and although the recovery of *H. americanus* stocks is not universal, some are now at a historic high and the fishery in the Gulf of Maine is now the most productive and valuable fishery in USA (Steneck and Wilson, 2001). Despite its high value and economic importance *H. gammarus* is not as well studied as *H. americanus* and much of what is know about *H. gammarus* is inferred from studies on the geographically separate *H. americanus*. Although both *Homarus* spp. are commercially important the scale of the two fisheries differ dramatically (142418 mt *H. americanus* compared to 4571 mt *H. gammarus* in 2013; F.A.O, 2016).

1.1.1 Homarus spp.

Homaridae are highly-mobile clawed lobsters that occur only in the North Atlantic Ocean, with no overlap between their native ranges. The native range of *H. americanus* is restricted to the western Atlantic coast, between Newfoundland, Canada and the North Carolina coast, USA (Cobb and Castro, 2006). *H. gammarus* has a wider distribution along the eastern Atlantic coast extending from the Arctic Circle to the north African coast (Triantafyllidis et al., 2005; Wahle et al., 2013). Illegal introductions and escapes of imported *H. americanus* have occurred and *H. americanus* are present in small numbers within European waters (Van der Meeren et al., 2000; Stebbing et al., 2012; F.A.O, 2016). Despite some visual similarities *H. americanus* appears redder and possesses a ventral tooth on the rostrum that is absent on *H. gammarus*. Although both species are genetically similar (Hedgecock et al., 1977) important differences do exist. *H. americanus* is more aggressive, more fecund, and although there are overlapping habitat requirements between the two species, *H. americanus* inhabitants a broader range of habitats than *H. gammarus* (Van der Meeren and Uksnøy, 2000; Van der Meeren et al., 2000), and a greater range of depths (100 m compared to 57 m; Hudon, 1994; Moland et al., 2011a).

Homarus spp. have an important and varied role within the benthic ecosystem (Boudreau and Worm, 2012) as prey (Oppenheim and Wahle, 2013; McMahan et al., 2013), scavengers (Hallbäck and Waren, 1972), and occasionally as dominant predators (Hagen and Mann, 1992; Hanson, 2009). The predation risk to lobsters decreases as they grow (Wahle and Steneck, 1992), and while early benthic phase *H. gammarus* are predated by small fish and crabs (e.g. *Ciliata mustela* and *Carcinus maenas* Ball et al., 2001), little is known about other natural predators of adult

H. gammarus. It is possible to infer possible predator types, that may pose a threat, from lobsters with a similar geographic range (Smith et al., 1998c), such as triggerfish, a predator of the Mediterranean slipper lobster *Scyllarides latus* (Barshaw and Spanier, 1994). Large ground-fish and sharks are known predators of *H. americanus* (Cooper and Uzmann, 1980) and day time predation by crabs has also been recorded (*Carcinus maenas* Oppenheim and Wahle, 2013). In areas where high population densities of *H. americanus* exist, and where numbers of natural predators like large predatory ground-fish have become depleted, nocturnal cannibalism among *H. americanus* can occur (Oppenheim and Wahle, 2013). Recent video footage showing escaped *H. americanus* within the native range of *H. gammarus* has confirmed the possibility of predation of *H. gammarus* by *H. americanus* (Øresland et al., 2017). There is a lack of information concerning *H. gammarus* diet composition, but it will depend on the availability and abundance of prey, the size of the individual, its moult cycle, and sea temperature, and likely include crabs, echinoderms, bivalves and carrion in varying proportions (Hallbäck and Waren, 1972). Some U.S. fisheries are likely sustaining *H. americanus* at inflated levels due to the large amount of bait being placed in the water (Grabowski et al., 2010).

1.1.2 Olfaction

As marine invertebrates, lobsters are generally assumed to have basic social structures and relatively simple behaviours (Karavanich and Atema, 1998a); however, both laboratory and field experiments have shown *Homarus* spp. to be capable of establishing and maintaining dominance hierarchies and visually recognising individual conspecifics (Karavanich and Atema, 1998a; Karnofsky and Price, 1989b; Kaplan et al., 1993; Gherardi et al., 2010). Relatively poor vision means that lobsters rely heavily on chemical signals released in urine that are subsequently modified in the olfactory pathway via sensors on the antennules and legs (Kaplan et al., 1993). Lobsters are prone to losing appendages (Scarratt, 1973), and overlap in chemosensory ability between appendages likely protects against loss of function (Devine and Atema, 1982). These chemical signals modulate behavioural responses including, aggression (Skog et al., 2009), mate selection (Atema, 1971; Skog, 2009b; Bushmann and Atema, 1997), and prey searching (Devine and Atema, 1982; Moore et al., 1991). Laboratory experiments have shown *H. americanus* capable of remembering a previously encountered dominant conspecific for up to 24 h, and in some instances, 1-2 weeks if the individuals were kept separately (Karavanich and Atema, 1998b).

When foraging, the source of an odour is located quicker when both sensors on the antennules and legs are used (Horner, 2004). The speed at which crustaceans track plumes indicate that they are not using time-average concentration

gradients (Webster and Weissburg, 2001), and instead use the spatial and temporal structure of the odour concentration to locate its source (Webster and Weissburg, 2009; Reidenbach and Koehl, 2011). The characteristics of a plume can determine a crustacean's success in tracking it, with greater success attributed to intermittent plumes (Weissburg and Zimmer-Faust, 1993), rather than those with more constant conditions. Distance olfaction and orientation when foraging primarily involves the chemoreceptors on the lateral antennules, as an individual approaches the source of a signal the chemoreceptors on the walking legs become increasingly involved in prey searching and recognition of the prey item (*H. americanus* Moore et al., 1991; Reidenbach and Koehl, 2011). Foraging success in a plume is affected directly by the speed of the flow and the degree of turbulence (Moore et al., 1991; Weissburg and Zimmer-Faust, 1993), but also the animals orientation and ability to move in increased flow conditions (Howard and Nunny, 1983; Weissburg and Zimmer-Faust, 1993).

If the release of urine by *H. americanus* males is blocked then visitations by females to male occupied burrows are shorter and less frequent (Bushmann and Atema, 2000); however, urine released in an empty burrow does not restore normal female behaviour indicating that more complex chemical signalling or sexual selection are involved. Although most of the studies of *Homarus* spp. mating behaviours have focussed on *H. americanus*, female *H. gammarus* are also able to differentiate between conspecific and heterospecific males when selecting a possible mate (Van Der Meeren et al., 2008). In a series of experiments where the antennules of both sexes of *H. gammarus* were ablated Skog (2009b) found that male olfaction in *H. gammarus* was necessary for intermoult matings as ablated males demonstrated fewer pre-copulatory behaviours and a significantly reduced number of matings; there was no significant difference between ablated females and non-ablated females. This suggests that a female sex pheromone is present throughout the moult cycle, and that female sexual behaviour may be influenced by other aspects of sexual selection (Skog, 2009b).

1.1.3 Habitat use

Homarus spp. have a strong association with shelter-providing habitat (Wahle and Steneck, 1992; Wahle, 1992b) and remain shelter-dwellers throughout their lives (Galparsoro et al., 2009). The early benthic phase of *H. gammarus* has proved particularly difficult to study and young-of-year individuals have still to be identified in the field (Linnane et al., 2001; Mercer et al., 2001). Although information on their abundance and distribution is lacking, habitat requirements are likely similar to *H. americanus* (Incze and Wahle, 1991; Wahle and Steneck, 1991) and linked to predation avoidance (Wahle, 1992a; Linnane et al., 2000), and avoidance of unfavourable conditions (Bertness et al., 1996; Sheehy and Bannister, 2002). Substrata with

pre-existing interstitial spaces are of particular importance (Linnane et al., 2000; Ball et al., 2001); both *H. gammarus* and *H. americanus* spend the majority of their first 2-3 years remaining within a shelter. Lobsters become increasingly free from predation pressure as they grow, their association with shelter weakens and large individuals become more mobile (Wahle and Steneck, 1992; Wahle, 1992a). Despite an increase in mobility of adult *Homarus* spp. seabed topography and habitats containing rocky outcrops continue to provide avoidance of predators and unfavourable environmental conditions such as strong currents (Howard and Nunny, 1983). The use of shelters to avoid predators increases during the pre-moult period and may result in increased interaction between animals (Karnofsky et al., 1989a); however, it is not clear if this is an indirect result of increased activity. *Homarus* spp. may select shelters that are proportional to their body size (Cobb, 1971; Dybern, 1973). Therefore the abundance, availability and distribution of suitably sized shelter can limit the size of individuals within a population (Howard, 1980). For example, larger individuals will be limited in their ability to excavate under rocky outcrops in soft substrate due to potential collapses (Howard, 1980). Similarly an area of many small rocks will provide a greater number of small potential burrows whereas a similar area of larger rocks will provide a smaller number of larger burrows (Caddy and Stamatopoulos, 1990). As such, crustaceans reaching a critical size may die, disperse, or if possible, limit growth in response to resource limitation, such as an inadequate number of suitably sized shelters (Beck, 1997; Bowlby et al., 2007).

Competition for shelters is a central part of the mating behaviour of both male and female *Homarus* spp. (Karnofsky et al., 1989a; Debuse et al., 2003) and a size difference between individual lobsters of as little as c. 5 % (c. 15 mm, carapace length (CL) range 84-115 mm) can determine the outcome of an aggressive interaction (Scrivener, 1971). *H. gammarus* males fight other males, and females will fight both females and males for occupancy of a shelter (Debuse et al., 2003). These agonistic interactions are particularly important as shelters enhance the guarding of the soft-shelled female, both pre and post-copulation (Karnofsky et al., 1989a), and protect against additional matings with competing males (Atema et al., 1979; Waddy and Aiken, 1986). Shelters are only shared by adults during the mating period (Ennis, 1984; Karnofsky et al., 1989a). Cohabitation of *H. gammarus* begins several days before the female begins moulting, mating takes place shortly afterwards; this usually takes place in the summer with ovigerous females appearing from September (Pawson, 1995). *H. gammarus* males that hold multiple shelters concurrently are able to attract more potential females (Debuse et al., 2003). However, at low shelter density female *H. gammarus* are attracted more by the size of a mate than their ability to obtain a shelter (Debuse et al., 2003).

The degree of shelter fidelity varies between individuals (Karnofsky et al., 1989a) and adult *Homarus* spp. are capable of evicting others (Karnofsky et al., 1989a; Scopel

et al., 2006). Evictions may be the result of local dominance or territoriality (Karnofsky et al., 1989a; Karnofsky and Price, 1989a). The defence and continued possession of a shelter may be the best option if shelters are energetically expensive to excavate or competition from conspecifics is high (Karnofsky et al., 1989b; Karnofsky and Price, 1989b), with owners potentially having a competitive advantage in disputes with intruders (Leimar and Enquist, 1984). Lobsters possess a fine-scale awareness of their surroundings and can use their tail-flip escape mechanism to move backwards towards the nearest shelter; if the entrance is blocked, they can move towards the next nearest shelter (Karnofsky et al., 1989a, *H. americanus*). Homing behaviour in lobsters is little studied (Vannini and Cannicci, 1995). Lobsters often return to a current shelter or one they have previously occupied, but the number of shelters used by a lobster is likely to vary seasonally (Ennis, 1984). Released lobsters have also been observed returning to the shelters where they were initially captured (Karnofsky et al., 1989a). If individuals return to occupy the same shelter after each foraging trip, rather than moving to a new one, they become central-place foragers (Orians and Pearson, 1979) and have to balance trade-offs between predation, distribution of foraging resources, time constraints and cost of locomotion. Homing could occur over large scales, particularly for *H. americanus* (Pezzack and Duggan, 1986). More generally it is likely to differ between juveniles and adults, be highly variable between individuals (Herrnkind, 1983), and depend on the availability of shelter-providing habitat of suitable dimensions.

1.1.4 Movement patterns

Studies have found *H. gammarus* movements to be relatively limited (Smith et al., 2001; Agnalt et al., 2007; Moland et al., 2011b; Wiig et al., 2013) with modest home-range sizes and long-term site fidelity (Moland et al., 2011b; Wiig et al., 2013). Smith et al. (2001) found that 95 % of *H. gammarus* recapture distances were less than 3.8 km from the original capture site and individuals inhabiting artificial reefs have been recaptured in the same location for more than 4 years (Jensen et al., 1994). Agnalt et al. (2007) also found that the majority of released females (84 %) moved less than 500 m and only a few moved farther than 1 km. In contrast *H. americanus* is known to exhibit both resident and dispersal movement patterns in response to resource availability (Watson III et al., 1999; Bowlby et al., 2007), with some inshore animals travelling more than 90 km from release sites (Campbell and Stasko, 1986) and individuals in offshore habitats, near the continental shelf, moving in excess of 100 km (Cooper and Uzmann, 1971). Ovigerous *H. americanus* are capable of undertaking deep-shallow water migratory movements in order to experience optimal water temperatures necessary for egg development to occur within a 9-12 month period (Campbell, 1986). Although small numbers of *H. gammarus* undertake longer distance movements of up to 45 km (Smith et al., 2001) the motivation and

frequency of these behaviours is not known, and there is no conclusive evidence for more than one movement related behavioural state (Moland et al., 2011b; Wiig et al., 2013; Skerritt et al., 2015). There is evidence that lobsters move differently on different substrates, undertaking faster more directional movement on sediment substrates compared to heterogenous rocky substrate (Skerritt et al., 2015), and potentially use sediment channels between rocky habitats to commute between preferred areas of habitat (Geraldi et al., 2009). *Homarus* spp. lobsters are mostly slow moving (mean *H. americanus* 0.9 m $min^{-}1$ (O'Grady et al., 2001)), although movement at speeds can reach 2.5 m $min^{-}1$; movement is generally considered to be undertaken in short bouts (Taylor, 1982). These measurements are from tank studies and movement under natural conditions would be expected to be highly variable and a function of the sampling rate.

Movement rates of both *H. gammarus* and *H. americanus* are both correlated with changing environmental conditions such as, water temperature (Smith et al., 2001; Bowlby et al., 2007; Jury and Watson, 2013) or salinity (Watson III et al., 1999), habitat suitability and availability of shelter (Howard, 1980). Movements of juvenile *H. americanus* are higher in contiguous cobble habitat than in habitat that is more patchy in its distribution (Hovel and Wahle, 2010). Seasonal changes in environmental conditions could be a driver of lobster movement due to density dependence associated with the changing availability of suitable habitats (Bowlby et al., 2007). Lobsters are ectothermic and seasonal variation in sea temperature means that activity is greatest in months associated with higher temperatures (Smith et al., 1998c, 1999, 2000; Moland et al., 2011b; Skerritt et al., 2015; Lawton and Lavalli, 1995). Significantly lower activity levels have also been observed during the day time (Smith et al., 1998c, 1999, 2000) and at shallower depths during the night (Moland et al., 2011a); this diel pattern in activity tracks changes in the timing of sunset and sunrise and therefore could be triggered by changes in light levels as day length varies seasonally (Smith et al., 1999). There can also be a relative increase in diurnal activity when high turbidity limits the levels of light reaching the seafloor (Smith et al., 1999) further supporting an effect of daylight intensity. A peak in activity in the hours immediately after sunset can be explained by a need for individuals to forage after a sustained period without food due to the limited opportunities in or close to their burrows (Smith et al., 1998c). The diet of adult lobsters includes prey items that may be more abundant and easily available at night (Hallbäck and Waren, 1972; Cooper and Uzmann, 1980) and therefore emergence could coincide with an increase in prey availability (Smith et al., 1998c). However, carrion and slow or sessile prey items (Cooper and Uzmann, 1980; Hallbäck and Waren, 1972) are available during the day suggesting day time shelter use is, at least in part, due to additional threats from visual predators (Smith et al., 1998c). For example, although individual movements by *H. americanus* are highly variable, they can reduce and expand the size of their

home ranges in response to the presence and absence of a predator (*Gadus morhua* McMahan et al., 2013).

There can be high individual variation in the movement patterns of *H. gammarus* (Moland et al., 2011b; Skerritt et al., 2015). Although several studies have been unable to identify a difference in the movement patterns between the sexes (Moland et al., 2011b; Wiig et al., 2013) a study using fine-scale spatial and temporal data (Skerritt et al., 2015) found that although core movement (50% utilisation distribution (UD)) patterns were similar, males moved further from shelter than females, and therefore had significantly larger home-ranges (95UD) and a greater likelihood of utilising multiple areas. Individual variability in the tendency to undertake longer range movements may also indicate differing 'personalities' (Gosling, 2001; Wolf et al., 2007) within populations where some animals are transitory and others are regarded as residents. Personalities have been observed in a wide range of taxa (e.g. birds (Garamszegi et al., 2009; Gabriel and Black, 2010)), mammals (Svartberg, 2005; Réale et al., 2009; Dammhahn, 2012), fish (Huntingford, 1982; Wilson and Godin, 2009; Chapman et al., 2011), cephalopods (Mather and Anderson, 1993) and cnidaria (Briffa and Greenaway, 2011; Rudin and Briffa, 2012)). Differences in an animal's predilection for more exploratory, risk-taking behaviour may stem from early life environment (Chapman et al., 2010), perceived predation risks (Bell and Sih, 2007) and food availability (van Overveld and Matthysen, 2010). However, these behavioural types within decapods have received little attention compared to cephalopods and vertebrates; most research is restricted to the hermit crab *Pagurus bernhardus* (e.g. (Briffa et al., 2008; Mowles et al., 2012)). These disparities between the movement patterns of lobsters could lead to unintentional targeting of particular life-histories within a fishery, if increased trap exposure results in an increased probability of capture.

1.2 Fisheries

In the UK *H. gammarus* are targeted as part of a mixed fishery along with brown crab *Cancer pagurus*, and to a lesser extent the velvet swimming crab *Necora puber*. Species are caught within the Northumberland fishery using baited two-chambered parlour traps that are deployed in strings from small and medium size vessels (<10 m Stephenson et al., 2017). Individuals enter the 'kitchen' chamber of the trap to access the bait, once the animal moves through to the second 'parlour' chamber the likelihood that the animal will escape from the trap is greatly reduced. Lobster traps only catch a small percentage of the animals that approach them (Karnofsky and Price, 1989a; Jury et al., 2001). Jury et al. (2001) found in a field-based experiment that of the *ca.* 300 *H. americanus* that approached the trap only 4 % entered and of those lobsters only 6 % remained in the trap and were captured. The more traps that are

within an individual's home range the lower the survival probability that individual may have due to a higher trap exposure rate (Wiig et al., 2013). The relationship between movement, habitat and catchability is still unclear. In a study by Geraldi et al. (2009) 80 % of *H. gammarus* were retrapped on the same substrate that they were originally captured on. Individuals were also more likely to be recaught by the same trap if initially caught on rocky substrate, compared to those trapped on sediment where catch rate was highest despite the highest densities occurring on rocky substrate (Geraldi et al., 2009). This may indicate a difference in catchability between those that move and those that do not. It is possible that bait plumes are 'funnelled' along channels of soft sediment and are easier to detect than those on rocky substrate (Geraldi et al., 2009; Tremblay and Smith, 2001; Weissburg and Zimmer-Faust, 1993). Dunnington et al. (2005) found that the relationship between substrate and catch rate was more marked for sub-legal($<$83 mm CL) than legal lobsters ($\geq$ 83 mm CL), where sub-legal lobsters were more consistently trapped on sediment, compared to legal lobsters that were not associated with one particular substrate. However, given the that smaller lobsters are more shelter dependent (Wahle and Steneck, 1992; Galparsoro et al., 2009) this association may be more related to the age-structure of the population, and habitat quality and availability than mobility (Wahle et al., 2013).

1.2.1 Stock assessment

Stock assessments of *H. gammarus* are often based on fishery-dependent data gathered via commercial fishers. These data provide low-cost information on both the distribution and the abundance of stocks, where abundance is expressed as catch per unit effort CPUE (Hilborn and Walters, 1992). In its simplest form CPUE is assumed to be proportional to abundance

$$\frac{C}{E} = Nq \tag{1.1}$$

where C is the catch, N is the stock abundance, E is the fishing effort, and q is a constant of gear efficiency i.e. the proportion of fishery captured by 1 unit of effort also known as the catchability coefficient (Ricker, 1975). This relationship assumes catchability is constant or varies around a constant mean (Quinn II and Deriso, 1999). This equation can be rearranged so that catch C is proportional to effort and a (negligible) fishing mortality (Hilborn and Walters, 1992)

$$C = qEN \tag{1.2}$$

Catchability is likely to vary spatially and with time, and this is particularly

problematic for crustacean fisheries (Miller, 1990). If trends in CPUE are ignored the resulting estimates could be biased and result in "hyperdepletion", where the stock is estimated to have declined more than it has, or "hyperstability" where it is estimated the stock has remained high, but has actually declined (Hilborn and Walters, 1992). The ability of traps to catch lobsters not only depends on gear design and selectivity (Elner, 1980; Krouse, 1989), but also environmental variables such as habitat composition (Tremblay and Smith, 2001), temperature (Fogarty, 1988; McLeese and Wilder, 1958) and current flow (Howard and Nunny, 1983), and can relate to individual qualities such as, size, sex and reproductive status. The distance between traps can also have an impact on the catch rate of each trap; if traps are too close and not independent of each other, the first and last trap of each string will have a higher catch rate due to a larger effective trapping area, i.e. reduced overlap with adjacent traps, (Smith and Tremblay, 2003). The assumption that trap catches are representative of the true population is one major limitation in using fishery-dependent data for stock assessment as the accuracy of catch rate, as a proxy for abundance, depends on how well other external factors that affect catch rate are understood (Maunder and Punt, 2004; Stoner, 2004). However, fishery-independent surveys of crustacean populations are usually time intensive, costly and difficult due to the cryptic nature and strong associations with shelter that are common throughout the lifecycle of many species (Addison and Bell, 1997; Smith and Tremblay, 2003). Many modelling approaches have therefore been developed to account for the well-known shortcomings of fishery-dependent data (Addison and Bell, 1997; Fogarty and Addison, 1997; Bell, 2001; Chen et al., 2005). However, the lack of information on how and where the postlarval stage *H. gammarus* are recruited to the benthos can create problems for stock assessments and has limited the success of studies aiming to quantify re-stocking programmes and the long-term enhancement of fisheries (Sheehy and Bannister, 2002; Linnane et al., 2001).

Many lobster fisheries consist of small independently owned boats operating within traditional areas or recognised territories (Turner et al., 2013). Lobster populations are often assumed to be stable (Bannister and Addison, 1986) including the Northumberland *H. gammarus* population (Cefas, 2017), but reactive management can fail to protect stock declines as seen in Norwegian stocks between the 1960s and 1980s (Dow, 1980); the Norwegian stock size and recruitment have been slow to recover despite increased regulation (Agnalt et al., 2007). The regional socio-economic importance of lobster fishing within coastal areas, means that any over-exploitation and resultant reactive management could severely impact fishers and their communities (Kafas et al., 2017). Currently the exploitation levels within the Northumberland fishery are very high (Cefas, 2017) and a greater understanding of stock and fishery dynamics would enable more proactive evidence-based management. However, as lobsters shed their exoskeleton at each moult period they

can not be aged with the same ease as fin-fish. Ageing can be determined using laboratory animals of known age or from growth rates derived from mark-recapture studies; while useful for the early stages after settlement this approach is ultimately limited by the increasing variability in individual growth rates as lobsters age (Wahle et al., 2013). The indeterminable age of lobsters limits the use of many of the widely available models of age-structured populations available for fin-fish fisheries (Smith and Addison, 2003; Punt et al., 2013). Biomass models are widely used, modelling biomass as a function of recruitment, growth and natural mortality; however, population age or size-structure is not included and therefore their usefulness is limited to monitoring change rather than detailed understanding of dynamic processes (Smith and Addison, 2003; Hilborn, 1997). CPUE is often used in biomass models, but can vary (e.g. seasonally Frusher and Hoenig, 2003; Ziegler et al., 2002, *J. edwardsii*), therefore the assumption of constant q is often violated resulting in stock size and fishing mortality being poorly estimated (Maunder and Punt, 2004; Miller, 1990). The biomass approach can be extended to include biological parameters and time-delayed processes, such as the delay between spawning and recruitment, and are known as delay-difference models (Hilborn and Walters, 1992). Although delay-difference models are age-structured they are not as complex as formal age-structured models, due to simplified assumptions in respect of growth, fecundity, survival and selectivity (Smith and Addison, 2003). Data poor stocks can be modelled using depletion models; however, depletion models also use CPUE, making them sensitive to any errors associated with q (Ricker, 1975; Miller, 1990). Current *H. gammarus* stock assessments (Cefas, 2017) use length-based cohort analysis (Jones, 1981, 1984) to estimate abundance and size selectivity from size-frequency data, assuming constant recruitment (equilibrium), all individuals are equally available to the fishery, and fishery data are accurate. The assumption of equilibrium is critical, and if violated data should be from a time period where there is no significant trends in recruitment or exploitation (Hilborn and Walters, 1992).

Integrated size-structured population models (e.g. *H. americanus* Chen et al., 2005) can be used in place of age-structured approaches and are similar to stage-structured population models in that each stage represents a different size class (Punt et al., 2013, 2016). The probability that the animal will grow, given its size, and move from one stage to another needs to be known, as well as the number of time steps between growth (the moult period) (Punt et al., 2016). These models can use data from a variety of sources and include tagging data from recaptured individuals to inform growth parameters (e.g. Siddeek et al., 2016) as well as environmental covariates (e.g. Cao et al., 2017). The width of each stage classification is important and the misclassification of immature versus mature animals can increase as bin-width increases (Szuwalski, 2016). The optimum number of size classes used to model populations is a current area of research, but is likely a trade-off between accuracy

and run time (Monnahan et al., 2016). The size and growth rate of crustaceans also varies spatially and temporally depending on environmental conditions and habitat availability (Howard, 1980), creating potential uncertainty associated with growth rate estimates (Punt et al., 2016). The spatial distribution of catch rate can provide useful management insights; however, as fish, and therefore fishing effort are rarely randomly distributed, indices of effort and abundance are often only indicative of localised areas (Walters, 2003). Integrating spatial effort data over time can result in strong assumptions about the state of stocks in lesser or unfished areas, and if trends in effort are ignored the resulting estimates will likely be biased (Walters, 2003).

1.2.2 Bait attraction

Although lobsters are not exclusively nocturnal, movement rates (Scopel et al., 2006) and consequently trap visitations (Watson III et al., 2009) tend to be higher at night, potentially affecting catchability (Bannister and Addison, 1986). Similarly, tagged *C. pagurus* (Skajaa et al., 1998) only responded to bait between 2245 and 0130, regardless of when traps were set, suggesting that diel rhythms influence susceptibility to bait, and that animals may only respond to chemical stimuli when in the appropriate physiological state. The motivational state of an individual may also influence its likelihood of approaching a trap; recently moulted individuals may approach a trap more readily than an individual that has not undergone ecdysis due to increased feeding activity in the post-moult recovery period (Zimmer-Faust, 1989). The type of bait used in the trap can determine the attraction to traps depending on its palatability, but also the size and strength of the bait plume it generates (Mackie et al., 1980). Higher temperatures can also result in an increase in activity rates and potentially an associated increase in catchability of lobsters due to an increase in their metabolic rate (McLeese and Wilder, 1958)

The problems associated with using fishery-dependent data for stock assessment and mark-recapture studies are relatively well known and several methods to standardise and address the heterogeneity in the probability of capture and reporting have been developed (Eggers et al., 1982; Smith and Jamieson, 1989; Bell, 2001). CPUE is routinely standardised using generalized linear or mixed models (Maunder and Punt, 2004); however, the success in standardising estimates will rely on how well the underlying conditions are described or understood, particularly those relating to fishing efficiency (Ye and Dennis, 2009). Understanding how the movement and activity of lobster varies overtime is important to improving our estimates of CPUE (Stoner, 2004). It is useful to consider capture as a two stage process. Firstly the lobster has to be present in, or move into, an 'area of bait influence' where the plume from the baited trap has a demonstrable effect on the individuals behaviour, or orientation. The individual then enters the 'trapping area' where the probability of

capture is > 0. The resulting 'catchability coefficient' (Miller, 1989, 1995, 1990) is assumed from the 'effective trapping area', a hypothetical area where the probability of capture is 1. However, determining the size of these hypothetical areas and the proportion of the population targeted is not straightforward (Miller, 1990; Bell, 2001). The CPUE of *H.gammarus* is considerably lower than crabs and can be less than 1% of *C. pagurus* CPUE (Bennett, 1974). Olfactory cues and navigational mechanisms are fundamental to how, why, and over what distance lobsters are attracted to baited traps, with area of attraction shaped by both the speed and direction of the current (McQuinn et al., 1988). The 'effective trapping area' may be smaller in locations with strong currents, perhaps due to currents diluting the bait odour plume (McQuinn et al., 1988). However, it can be difficult to disentangle the effect of current speed on the area of bait influence as many marine benthic animals, including lobsters (Howard and Nunny, 1983), move less under these conditions, affecting catchability.

Data gathered using tracking technologies has allowed individual responses to baited-traps to be identified, through either a change in speed of an individual (Skajaa et al., 1998) or an acuteness in the change of direction (≥ 30 degrees) (Watson III et al., 2009); an approach to a baited-trap without a change in speed or direction of travel would constitute no response to the bait. Average time spent by lobsters at traps can range from 81 min (range 10 min - 720 min) (Watson III et al., 2009) to 230 min (*P. cygnus* (Jernakoff and Phillips, 1988)). Due to the potentially large distances moved more field-based studies are needed to fully describe the range of movement behaviours in response to bait under different environmental conditions, and population densities (Stoner, 2004).

1.2.3 Behavioural interactions

Trap saturation is the reduction in the effectiveness of a trap as the catch increases (Beverton and Holt, 1957). Conspecific and heterospecific behavioural interactions in and around traps can affect catchability (Addison, 1995; Jury et al., 2001). Traps pre-stocked with *H. gammarus* of either sex have a lower catch rate as individuals are less likely to enter a trap if it is already occupied by a conspecific (Addison, 1995; Jury et al., 2001). Richards and Cobb (1983) found a reduction in catch of 43 $\%$ and 65 $\%$ for *H. americanus* over 24 h when traps were pre-stocked with three or eight individuals, respectively; CPUE was also reduced for both *Cancer borealis* and *Cancer irroratus*. Traps do not catch very small lobsters that can easily escape; catchability of lobsters can increase with size (*H. americanus* Ennis, 1978; Miller, 1995), and potentially differ between the sexes (Miller, 1995). Therefore, the relationship between catch and abundance weakens as lobsters increase in size (Watson and Jury, 2013). Individuals exhibiting size-related dominance can evict

smaller individuals, or if already in the trap, they can prevent smaller individuals from entering (Jury et al., 2001). For this reason the maximum capacity of a trap is unlikely to be realised. If other animals are deterred from entering a trap due to the presence of an individual then CPUE is no longer linearly related to stock abundance and could lead to biased stock assessments (Addison, 1995). CPUE can also be affected by the immersion period or 'soak time' of the trap (Bennett, 1974; Lovewell et al., 1988; Miller and Rodger, 1996) and while catch rate can increase with soak time, it does so non-linearly (Lovewell et al., 1988). The timing of trap saturation will also likely vary with the size of lobsters caught. Smaller lobsters may be attracted first and larger, less abundant, more mobile lobsters attracted later in the soak (Watson and Jury, 2013). As catch is known to be asymptotic with soak time (Miller, 1976) short soak times are often advocated (Miller and Rodger, 1996). These behavioural interactions could lead the distribution of individuals to appear random when the true population may be more aggregated (Addison and Bell, 1997). Behavioural interactions may also have a greater influence on the catchability of lobsters than depletion of local stock in the vicinity of the trap, or the decline in bait attractiveness, that occur during the duration of the soak time (Addison and Bell, 1997).

1.2.4 Management strategies

H. gammarus landed in the UK are subject to a minimum landing size (MLS) of 87 mm CL, but larger MLS can occur regionally; Devon & Severn, Cornwall, and Isles of Scilly all enforce an MLS of 90 mm CL. These MLS attempt to prevent the landing of immature individuals and maximise the yield per recruit (Gendron, 2005). However, it is likely that the truncation of the true size distribution still occurs as larger animals are harvested. The size at which individuals reach maturity can vary between populations (Lizárraga-Cubedo et al., 2003), and there is evidence that a decrease in size at maturity of female lobsters in Canadian fisheries is an evolutionary response linked to long-term exploitation (Haarr et al., 2018). Additional management measures to boost the reproductive potential of stocks include 'v-notching' and a ban on the landing of ovigerous females. V-notching involves removing a triangular area from the uropod from reproductive size females, this area remains visible for approximately two moult cycles during which time the landing of these marked individuals is banned (Acheson and Gardner, 2011). In areas where recruitment is limited, this has proved successful in boosting the reproductive potential of stocks (Tully, 2001).

In England the management of fisheries that exist within 6 nm are managed by ten Inshore Fisheries and Conservation Authorities (IFCAs); IFCAs are also responsible for Marine Conservation Zone (MCZ) management. The Northumberland Inshore Fisheries and Conservation Authority (NIFCA) release approximately 1000 v-notched

female lobsters annually, these individuals are bought from wholesalers and released throughout the NIFCA district (NIFCA, 2017). A total of 20174 animals have been released since the scheme began in 2000, and additional informal v-notching is carried out by fishers at sea; in 2017 90 % of v-notched females were ovigerous (NIFCA, 2017). The landing of shellfish parts, mutilated individuals (e.g. missing uropods which may obscure v-notching), and soft-shelled individuals is also banned. There has been an increase in trap-fishing effort in recent years, and an increase in catch between 2001 and 2014 (Stephenson et al., 2017). This is potentially due to declining finfish populations resulting in an increase in fishers targeting shellfish (Molfese et al., 2014). Since 2009 the number of traps that can be fished per vessel within NIFCAs jurisdiction has been limited to 800, the impact of this on fisher behaviour is likely to be limited (Stephenson et al., 2018) as fishers may increase their effort to reflect management limits (Acheson and Brewer, 2003). A female biased sex ratio for lobsters has been previously identified (Thomas, 1955). However, this is not apparent from commercial catches where both sexes are equally represented (Mesquita et al., 2017). If there was a sex bias within a population, a behavioural difference between the sexes that increased the catchability of the underrepresented sex, such as increased movement, could mean that the skewed population composition would be undetectable in the fishery (Skerritt, 2014). There is some preliminary evidence of a female skewed sex ratio in the Northumberland lobster population from mark-recapture data, but these findings have not been validated using diver surveys and should be interpreted cautiously (Skerritt, 2014).

1.2.5 Marine Protected Areas

Marine Protected Areas (MPAs) and Marine Conservation Zones (MCZs) are designated areas for the protection of marine habitats and or species of conservation importance. These designations can include 'no-take zones' that exclude all fishing activities, both recreational and commercial, as well as areas with restricted activity offering partial protection (e.g. recreational fishing only). The main objectives of these designations are species recovery or habitat regeneration in the complete or partial absence of anthropogenic pressures. MPAs can increase the CPUE and biomass of *H. gammarus* (Moland et al., 2013). The degree to which marine reserves can benefit commercial fisheries has in the past been unclear due to the lack of appropriate control sites and spill-over effects are hard to demonstrate without comparative measures of emigration and immigration from control areas (Moland et al., 2013; Goñi et al., 2010). There is a potential confounding effect that high quality habitat is more likely to be afforded protection and that the increase in biomass or productivity is related to habitat and not to the degree of protection awarded (Gell and Roberts, 2003). 'No-take zones' have proved successful in increasing the survival, abundance and or biomass of several commercially valuable lobster species: *H.*

gammarus (Sainte-Marie et al., 2011), *H. americanus* (Rowe, 2002), spiny lobster *Jasus edwardsii* (Kelly et al., 2000; Shears et al., 2006); however, partial protection (i.e. recreational fishing only) has proved less successful (Shears et al., 2006). Quantifying animal movement is key to understanding the spatial requirements necessary to fully protect populations of highly mobile species (Grüss et al., 2011b; Di Lorenzo et al., 2014) and further work is required. A lack of data on the spatio-temporal dynamics of spill-over and recruitment effects for many target species limits the understanding of the true potential of MPAs and MCZs as conservation tools (Sale et al., 2005).

1.2.6 Artificial reefs

Artificial reefs can provide suitable habitat for a range of species potentially limited by the availability of hard substrate such as shelter-seeking fish (Hixon and Beets, 1989), and several lobster species, for example *H. gammarus* (Jensen et al., 1994), *H. americanus* (Scarratt, 1968; Miller et al., 2006), and *Panulirus argus* (Davis, 1985; Sosa-Cordero et al., 1998; Briones-Fourzán and Lozano-Álvarez, 2001). As a result they have the potential to enhance habitat, or mitigate for habitat loss (Davis, 1985; Reynolds et al., 2010); however, benefits are likely to be habitat and size-class dependent (Gutzler and Butler IV, 2015). Artificial reefs vary in their size, configuration and in the materials used, with many made of waste materials (Collins and Jensen, 1997). Artificial reefs can be effectively colonised by *H. gammarus* even if isolated from similar hard substrate (Jensen et al., 1994; Jensen, 2002), and can hold many long-staying individuals that reproduce (Jensen et al., 1994). Given the known relationship between *Homarus* spp, substrate and shelter size (Howard, 1980; Miller et al., 2006), reefs could be created to target specific sizes of lobsters that might be experiencing a habitat bottleneck (Caddy and Stamatopoulos, 1990; Beck, 1997).

Anthropogenic structures have also been found to provide favourable habitat for decapod crustaceans including *H. gammarus* (Langhamer et al., 2009; Wehkamp and Fischer, 2013). The closure of fisheries due to wind farm construction can provide a respite opportunity for stocks, by increasing abundance and the size distribution of the population in the short term (Roach et al., 2018). However, outcomes can be mixed depending on the species and the range of habitat types provided, and results can be confounded by predation, environmental variables and detectability (Wehkamp and Fischer, 2013).

1.3 Technologies and current methodology

1.3.1 Telemetry

Previously the ability to conduct long-term mark-recapture studies on lobsters was limited due to animals losing externally attached tags at ecdysis (Thomas, 1955;

Gibson, 1967), limiting identifiable recaptures to within 1 year of the initial release. The main aim of these studies was to provide information on the fishing mortality or growth rate of individuals, although they did provide limited information on the movement of marked individuals (Thomas, 1955; Gibson, 1967); the majority of recaptures were close to the original capture site at a maximum distance of 8 km. The development of 'persistent tags' that are attached through the dorsal muscle (Gundersen, 1962; Jensen et al., 1994; Watson III et al., 1999; Smith et al., 2001) allows wild lobsters to be studied over longer time periods and potentially greater distances in their natural habitat (Smith et al., 2001). Traditionally lobster activity studies have taken place in the laboratory (Mehrtens et al., 2005), mesocosms (Watson III et al., 2009), or have used SCUBA surveys to observe behaviour and survey lobsters (Karnofsky et al., 1989a; Cobb, 1981). The sustained effort required for focal sampling of behaviour, and the nocturnal and cryptic nature of lobsters can make these types of study difficult.

Radio-telemetry has been long been used as a successful method to collect data on movement and behaviour in terrestrial habitats (e.g. LeMunyan et al., 1959). However, the use of underwater telemetry was slower to develop (Hockersmith and Beeman, 2012) and while some semi-terrestrial and freshwater species have been tracked successfully using radio telemetry (Robinson et al., 2000) the applications for this method in the marine environment are limited due to the increasing attenuation of radio signals with conductivity and depth. As sound travels at a predictable speed through water, acoustic telemetry has proved a more reliable method for tracking marine animals; the distance travelled by an acoustic signal can be calculated from the time it takes the signal to reach the receiver (hydrophone) (Watkins and Schevill, 1972). Acoustic telemetry has now become extremely popular (Hussey et al., 2015) and several systems and configurations are available depending research needs (e.g. VEMCO Ltd and Lotek Wireless Inc.). Modern systems (e.g. Vemco Positioning System, Vemco Ltd, Halifax, Canada) recommend a full range test using a series of control tags to assess impacts on positional errors and detection rates. If a project continues through more than one season, repeated range tests, or permanently deployed control tags, are used in order to avoid under or over estimating detection rates (Mathies et al., 2014; Smith et al., 1998a). Electromagnetic telemetry provides a possible alternative for animals that are relatively sedentary; however, the short detection range (a few metres), the need for cables on the seafloor and more specific tag design requirements, limited its wider application (Smith et al., 2000), and it has now largely been superseded by acoustic telemetry devices.

Although trade-offs still exist for the smallest of animals, the extended battery life and small size of many modern tags, including acoustic telemetry tags, mean that animal movements can now be studied in near continuous time at a fine spatial scale (error $<$ 10 m) (Urbano et al., 2010; Kie et al., 2010; Tomkiewicz et al., 2010). The majority of

lobster acoustic telemetry studies have used manual unidirectional hydrophones to monitor movements (Watson III et al., 1999; Moland et al., 2011b), or a fixed hydrophone within a mesocosm (Watson III et al., 2009). By using a fixed array of omnidirectional hydrophones, continuous multiple fixes are remotely obtained from tagged lobsters that remain within the array. Each acoustic tag transmits at a unique frequency so that the positions of tagged individuals can be differentiated for analyses. Acoustic tags can be fitted to the large crushing claw of the animal with a harness made of a plastic cable tie and a short piece of plastic tubing that allow the tag to remain in place and not impede movement (Moland et al., 2011b). Once the tagging procedure is complete and the lobster is released, all changes in activity and position can be recorded at the desired sampling rate without further disturbance or need for recapture. Although this method produces a large amount of data with high spatial and temporal resolution, it is dependent on the lobster remaining within the predetermined array. If animals move out of the array no further data will be collected for those individuals; while fixed arrays provide an excellent method for studying small-scale local movements, movements over greater distances by individuals may result in a loss of that individual from the study population. Communication with the tagged lobster may also be lost temporarily if it conceals itself in a burrow or under a rock, but tracking will resume once the lobster re-emerges. Again, a range and configuration test can assist in identifying suitable receiver placement so as to avoid 'dead patches'.

1.3.2 Current data analysis techniques

Advancing tracking technologies are producing large amounts of spatially-explicit data. New and innovative methods of analyses are required (Cagnacci et al., 2010) so that high-resolution individual-based data can be scaled-up to infer population level effects useful for informing management decisions (Michelot et al., 2018; Allen and Singh, 2016). Tagging systems now provide almost continuous tracking, resulting in highly autocorrelated data (Fieberg et al., 2010), and challenges remain on how best to match the spatial and temporal resolution of such movement data to that of the environmental covariates (Remelgado et al., 2017). Although measurement error associated with tracking technologies are now often < 10 m the error to signal ratio could still be large for smaller animals, or those that move infrequently within a restricted area (Hurford, 2009).

Previously autocorrelation has been regarded as a useful indication of the biological importance when assessing home-range estimates (de Solla et al., 1999; Fieberg, 2007), or addressed directly by subsampling data to a temporal resolution appropriate for independence (Turchin, 1998; Swihart and Slade, 1985). It is likely more appropriate to use techniques that can model autocorrelation and may elucidate the ecological

patterns and relationships within these data (Dray et al., 2010; Rooney et al., 1998; Gurarie et al., 2009). Particularly as the high levels of autocorrelation within tracking data may change in relation to behaviour and environmental conditions; as a result subsampling to independence could potentially over or underestimate autocorrelation at different time periods (Rooney et al., 1998).

High-resolution tracking means that analyses of animal tracking data has moved away from considering isolated points in space towards considering time series of animal movement. In addition to more traditional static measures of space use such as kernel density estimation (Millspaugh et al., 2006) and minimum convex polygons (MCP) (Mohr, 1947) space-sharing and behavioural interaction can now routinely be assessed in the context of space and time (e.g. dynamic interaction, Long and Nelson, 2013; Benhamou et al., 2014) providing a means to investigate how the locations of individuals interact. High-resolution tracking data can be used to derive bivariate time series consisting of step lengths and turn angles of animal movement (Turchin, 1998) that can be analysed to infer biologically relevant behavioural states (Jonsen et al., 2005; Langrock et al., 2012). State-space (Jonsen et al., 2005) and hidden Markov models (HMM) (Langrock et al., 2012) seek to classify movement data by estimating the step length and turn angle distributions each observation belongs to. For example, foraging behaviour is characterised by tortuous movement and short step lengths and more exploratory behaviour encompasses more directional movement and longer step lengths (Morales et al., 2010). HMMs provide a more tractable approach than the often computationally intensive Bayesian inference (Langrock et al., 2012; Michelot et al., 2016a). HMMs have been used to study the movement of a wide variety of taxa: American bison (*Bison bison*) (Langrock et al., 2012), grey mouse lemurs (Schliehe-Diecks et al., 2012), caribou (*Rangifer tarandus*) (Franke et al., 2004), red-cockaded woodpecker (*Picoides borealis*) (McKellar et al., 2015), and Florida panther (*Puma concolor coryi*) (van de Kerk et al., 2015). Marine species have also been successfully modelled: southern bluefin tuna (*Thunnus maccoyii*) (Patterson et al., 2009), white sharks (*Carcharhodon carcharias*) (Towner et al., 2016), and southern elephant seals (*Mirounga leonina*) (Michelot et al., 2017).

It is assumed that each observation in an animal's movement path is generated from N distributions, the distribution selected at each time step is determined by a sequence of finite states, in this context these states reflect animal behaviour. This sequence of events is modelled using a Markov chain, and as such, the probability of transitioning between states is only dependent on the current state, i.e. first-order dependence (Zucchini et al., 2016) (Fig. 1.1). Model parameters can be assumed to be either the same for all individuals, or individual-specific; the former does not allow any individual variation and the later involves a larger number of parameters and comparisons of movement processes between individuals (Langrock et al., 2012). Hierarchical approaches, where individuals share some model parameters, exist for

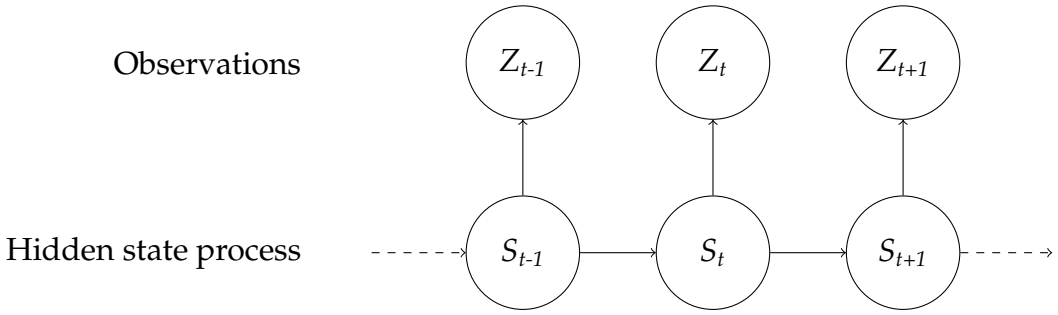

Figure 1.1: Dependence of a hidden Markov model, modified from (Michelot et al., 2016b)

both Bayesian (Jonsen et al., 2005; Eckert et al., 2008; Jonsen, 2016) and for likelihood based HMMs (Schliehe-Diecks et al., 2012).

These ever increasing amounts of fine-scale spatial and temporal data have begun to be used within some fisheries to develop a more dynamic management of marine resources (Maxwell et al., 2015). Up-to-date tracking data can provide information on changing habitat predictions, so that quota allocations can be updated to avoid over-explotation (Hobday et al., 2011), and by-catch avoidance can be improved (Zydelis et al., 2011). Whilst these approaches are not necessarily applicable to the relatively site faithful *H. gammarus*, acoustic telemetry does provide a means to study movement and behaviour under realistic conditions that could not be achieved in aquariums and mesocosms. Tracking technologies have great potential to improve fisheries management (Crossin et al., 2017), but a careful balance has to be found between the protection of vulnerable species and exploitation of targeted stocks (Maxwell et al., 2015).

1.4 Conclusion

There are many similarities between the life histories of *H. americanus* and *H. gammarus*; however, the scale of the fisheries differ dramatically. The relationship between lobster movement and catchability is poorly understood for both species, but given the apparent differences in the magnitude of movements undertaken, inferring knowledge of the drivers of *H. gammarus* movement from that of *H. americanus* would be unwise. Lobster populations may be assumed to be stable, but estimates rely on the often violated assumption of a proportional relationship between CPUE and abundance. A more in depth understanding of how current levels of exploitation are impacting population dynamics is limited by a lack of information on early benthic phase recruitment. Current estimates could be improved by gaining greater understanding of how catchability and movement varies within a population. If

sustainable, regionally managed, evidence-based fisheries are to be successful then the knowledge gaps that still surround the spatial ecology, behavioural interactions and population structure of *H. gammarus* need to be addressed.

1.5 Aims of thesis

The overall purpose of this thesis is to address knowledge gaps surrounding the spatial ecology and movement behaviour of *H. gammarus* using fine-scale acoustic telemetry. The work within this thesis also goes some way to evaluating the suitability of acoustic telemetry data for studying the behaviour and fine-scale movements of benthic invertebrates, and highlights some areas where future technological and statistical developments are necessary.

The aims of this thesis are to:

1. to quantify *H. gammarus* movement patterns in the presence and absence of baited traps, and their behaviour in the vicinity of a baited trap
2. to quantify spatial-overlap, space-sharing, and interaction between *H. gammarus* in the absence of fishing
3. to identify different behaviour states and investigate the environmental drivers of *H. gammarus* movement
4. to investigate the influence of the tides and the distribution of *H. gammarus* on their catchability within a Northumberland fishery

1.6 Thesis outline

Chapter 2 investigates the behaviour of lobsters in the absence and presence of baited traps, and uses null models to differentiate random from non-random movements, and behaviour in the vicinity of baited traps. Chapter 3 quantifies the spatial overlap and space sharing between individual lobsters at multiple spatial scales and attempts to identify fine-scale behavioural interaction between pairs of individuals. Chapter 4 uses behavioural change point analysis to identify different movement states, and hidden Markov models to identify environmental drivers of movement. Chapter 5 uses an individual-based model to investigate how the probability of transitioning between two movement states might change across the tidal cycle and affect the catchability of individuals. A series of model scenarios use different parameters to assess the effect of current speed, bait amount, and bait decay on the probability of capture. The final chapter of the thesis, Chapter 6, highlights the most important findings from the thesis and suggests further areas of research interest.

You can't expect a demigod to beat a decapod.

Tamatoa

Declaration

Chapter 2: *The movement and behaviour of European lobster around baited traps* is published as K. J. Lees, A. C. Mill, D. J. Skerritt, P. A. Robertson, and C. Fitzsimmons, Movement patterns of a commercially important, free-ranging marine invertebrate in the vicinity of a bait source, Anim. Biotelemetry, pp. 1–12, 2018.

Chapter 2. The movement and behaviour of European lobster around baited traps

2.1 Introduction

Catch per unit effort (CPUE) is widely used within fisheries management as a measure of both catch and effort, information that is necessary for fitting many fisheries stock assessment models (Hilborn and Walters, 1992). CPUE is usually based on data collected by fishers, and provides a convenient, low cost proxy for relative abundance. However, inherent biases exist within these data and the true relationship between abundance and catch is often unknown (Bennett, 1974; Addison and Bell, 1997). As such, the assumption of linearity between catch and abundance is often violated (Maunder and Punt, 2004) and the appropriateness of CPUE as a proxy for abundance relies on accounting for changes in catch over time that are not the result of changes in abundance (Hilborn and Walters, 1992; Maunder and Punt, 2004). Methods to standardise CPUE have been available for many years (Beverton and Holt, 1957); generalised linear models, and mixed effects models are now commonly used (Maunder and Punt, 2004). However, knowledge gaps still exist regarding the ecology, behaviour, and movement patterns of many commercially important species, and the likelihood of capture is commonly assumed to be equal across all demographics. Consequently, information that could improve the accuracy of CPUE and therefore stock assessments of these species is not always available. Improved abundance estimates in baited trap fisheries will rely on better understanding of the capture process, including attraction to a bait source, so that the probability of attraction and the proportion of the population targeted can be more accurately quantified (Miller, 1990).

H. gammarus are an economically important species within the United Kingdom (UK) and throughout its range, for example UK landings by UK vessels were worth £39.5 m in 2016 (Marine Management Organisation, 2017). Despite its commercial value much of what is known about its ecology is derived from the closely related *H. americanus*. *H. gammarus* are typically fished using strings of multiple two chambered traps, known as parlour traps, these consist of a baited area entered through a tunnel, and a subsequent area that makes escape from the trap unlikely. *H. gammarus* often form a mixed fishery, commonly with *Cancer pagurus*, and as a result any number of intra and inter-specifics can be attracted to the baited static traps. Subsequent behavioural

interactions affect the probability of attraction, and the probability of entering the approached trap (Richards and Cobb, 1983; Addison, 1995; Addison and Bell, 1997). The proximity of preferred habitats (Karnofsky and Price, 1989a), and the selectivity and immersion time of a trap (Elner, 1980; Krouse, 1989; Bennett, 1974), will likely determine the number of lobsters attracted and subsequently trapped (Tremblay and Smith, 2001; Bowlby et al., 2007). However, lobster movements and therefore trap encounters are affected by a number of time-varying environmental conditions, such as seasonal changes in water temperature (Miller, 1990; Fogarty, 1988; Smith et al., 1998c, 2001, 1999; Robertson et al., 2016) and periodic variation in current speed (Moore et al., 1991; Moore and Atema, 1988; Howard and Nunny, 1983). The motivation of individuals to respond to potential food sources can also be affected by internal physiological states relating to moult and the associated predation risk (Karnofsky et al., 1989a), reproduction, and hunger regulation (Zimmer-Faust, 1989; Karnofsky and Price, 1989a). It is the interplay between these factors that vary at both the individual and population level, and across multiple spatial scales, that make calculating the effective trapping area particularly difficult (Bell, 2001; Miller, 1990).

Lobsters primarily identify and navigate towards potential sources of food using their highly developed olfactory system (Derby and Atema, 1982; Devine and Atema, 1982). Despite being well studied (Atema, 1995; Derby and Atema, 1981; Moore et al., 1991) it remains unclear over what distance a bait plume remains detectable, as chemical signals are mixed and degraded by environmental processes (Moore et al., 1991; Atema, 1995). A number of studies have been undertaken in aquariums (Karnofsky and Price, 1989a; Shelton, 1981; Moore et al., 1991) where the direction and speed of current, and the degree of mixing can be carefully controlled. Alternatively, studies have been conducted in mesocosms (Scopel et al., 2006; Jury et al., 2001; Watson III et al., 2009) that can exclude potential sources of 'background' stimuli, that may confound an observable olfactory response, and can control the density of animals within the study area. While these enclosed environments provide greater experimental control they can lack realism and restrict movement.

The distance over which a bait plume might be detected is determined by both the speed and direction of the current (McQuinn et al., 1988) and can vary considerably depending on the target animal (Watson III et al., 2009; Skajaa et al., 1998; Jernakoff and Phillips, 1988). Attempts to identify responses to bait sources have focussed on the orientation of individuals in relation to the prevailing current, and have often resulted in uncertainty due to heterogenous conditions (Skajaa et al., 1998; Watson III et al., 2009). Changes in behaviour in response to a trap have been identified by a notable change in direction (Watson III et al., 2009), or by a change in speed (Skajaa et al., 1998, *C. pagurus*). *H. americanus* has been previously shown to slow down when approaching an odour source, however these experiments were undertaken within an aquarium and the scale of movements are not directly comparable (Moore et al.,

1991); no change in speed has been identified in the field (Watson III et al., 2009). One particular drawback of free-ranging studies is that it is more challenging to definitively relate movement towards a trap to the traps presence, due to the logistical difficulties in validating the behaviour of marine animals. However, by comparing a measure of trap approach generated from the observed data, to one generated under random movement it is possible to infer whether an approach was non-random, and in part reduce uncertainty regarding the relationship between the movement, and the presence of the trap. The null model approach (Gotelli and Graves, 1996) has been widely used within ecology. Null distributions, generated by resampling or randomisation, provide data without biological mechanism or process. Observed values can then be compared to expected values derived from the null distribution; care is required when specifying the degree of randomness of null distributions so as to avoid Type I (Wilson, 1995), or Type II (Colwell and Winkler, 1984) errors.

The aim of this study was to investigate the behaviour of free-ranging *H. gammarus* in the vicinity of baited commercial parlour traps, and the distance of attraction to baited commercial parlour traps. The null hypothesis was that there would be no change in lobster behaviour in the presence and absence of traps, and no relationship between current speed and the distance of attraction to a trap (Watson III et al., 2009). A further null hypothesis, that patterns in lobster movements in relation to baited traps were random, and that changes in measurable behaviour, such as turn angle and step length, were independent of the traps presence, was tested using a null model approach.

2.2 Methods

2.2.1 Data collection

A VEMCO Positioning System (VPS), (AMIRIX Systems Inc., Halifax, Canada) was deployed approximately 2 km off Blyth, Northumberland (55.1270° N, 1.5103° W) on the 7th of April 2016, (Fig. 2.1) covering approximately 1.5 km^2. The depth of the study site ranged from approximately 19 - 29 m. A string of 20 commercial parlour traps was set within the study area on the 30th of March 2016 and hauled after approximately 24 h. Traps were reset and hauled again after 7 days. Fourteen lobsters were caught (carapace length 71-92 mm, 8 females and 6 males) and fitted with a VEMCO Ltd. V13 acoustic transmitter (weight in water 6 g, 1 % of body weight). Transmitters were attached above the crusher claw using a harness (Fig. 2.2, Moland et al., 2011b) and were set to transmit every 200-400 s (frequency 69 kHz). Tagging of lobsters took less than 10 min and all tagged individuals were released immediately within the study site.

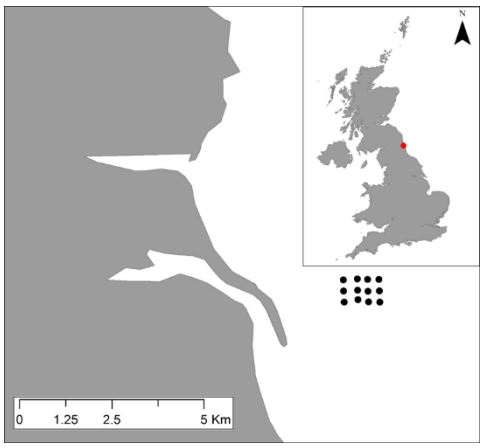

Figure 2.1: Study site. United Kingdom, inset: Blyth Harbour (red dot), VEMCO Positioning System hydrophones (black dots).

Figure 2.2: A lobster fitted with a V13 acoustic transmitter.

2.2.2 Experimental traps

Twelve separately moored commercial parlour traps were placed across the range of substrates available within the study site. Substrate was characterised using an Olex AS (www.olex.no) echosounder that provided a measure of relative substrate hardness on a linear scale of 1-100, where 100 would represent 0 energy loss and therefore higher values were associated with more reflective substrates. These data were subsequently classified as, 'Soft', such as mud < 60, 'Mixed', such as mud and rock > 60 and < 80, and 'Hard', such as continuous rock > 80. It is not possible to infer habitat type using this method as substrate roughness is not measured (Elvenes et al., 2013), however these data are a broad indicator of substrate type and have been previously validated using drop-down cameras in the vicinity of the study site (Skerritt et al., 2015). Trap locations within each substrate were chosen randomly, although an effort was made to avoid areas close to hydrophone moorings and ground lines to avoid entanglement and displacement of hydrophones. All traps were baited with approximately 300 g of whiting *Merlangius merlangus* and plaice *Pleuronectes platessa* in equal proportions; traps were placed at least 50 m apart (Smith

and Tremblay, 2003) to minimise adverse interactions and competition from overlapping trapping areas (Bell, 2001). Traps were also tagged prior to deployment, so that trap locations within the study site were known. Traps were deployed with the entrance closed to avoid retrapping tagged lobsters and the possible effects of trap saturation on lobster behaviour (Miller, 1976; Miller and Rodger, 1996; Addison and Bell, 1997). Traps were deployed on the 3rd of May 2016 and were subsequently rebaited and moved to new locations on the 12th and the 24th of May 2016. Only ten traps were redeployed during the 3rd deployment as two became detached from their marker buoy sometime during the 2nd deployment. A current meter (Nortek Aquadopp 3000 m) was deployed in the centre of the array between the 12th and 27th of May to collect current speed and direction every 10 min.

2.2.3 Data pre-processing

Prior to analysis detections with high positional error were identified using linear regression between two measures of horizontal positioning error (HPE and HPEm) (Skerritt et al., 2015; Coates et al., 2013). The model was weighted by the number of HPEm observations per whole value of HPE. This was to account for the exponential decline in the number of observations as the value of the HPE increased. Observations with a HPE greater than 24 were removed, limiting the maximum error to approximately 23 m. There was evidence of commercial fishing within the study site. To reduce the possible confounding effects of non-study fishing gear, only lobsters that were detected within 20 m of a study trap location during the first 72 h of its deployment were considered to have approached a trap and were included in the analyses. These criteria show consideration of the positional error associated with the data and reduce the likelihood that approaches not initiated by a bait plume were included. Lobster positions recorded between the 7th of April and first trap deployment on the 3rd of May were considered 'pre-trap' data. 'Post-trap' data were defined as positions recorded in the 72 h immediately following deployment of each trap. Data were projected in Universal Transverse Mercator (UTM) Zone 30 using ArcMap 10.2 (Esri) and movement metrics were calculated using Geospatial Modelling Environment (Beyer, 2012). Lobster speed was estimated as the distance between positions at time t and $t + 1$ divided by the associated detection interval.

2.2.4 Data analysis

Analyses were conducted using R (R Core Team, 2017). To investigate the direction of lobster movement in relation to the prevailing current direction the time stamps of the lobster data were rounded to the nearest 10 min period and then matched to the corresponding current data. If the difference between the lobsters bearing and the current direction was between 150° and 210° the lobster was assumed to be moving

'against' the current (i.e. in the opposite direction). A turn towards the trap was defined as a turn greater than 30° (Watson III et al., 2009) that resulted in the lobster being detected within 20 m of the trap; the distance from the trap that this turn occurred was defined as the distance of attraction. If a turn towards the trap also resulted in movement against the current it was considered a potential response to a bait plume. If a lobster reapproached within 5 m of the trap it was not considered a separate approach. Trajectories were visually assessed using the *trajdyn* function of the R library AdehabitatLT (Calenge, 2006) to verify that the lobsters position relative to the trap and associated bait plume. Linear mixed models were used to investigate the relationship between distance of attraction and current speed, time since deployment and the sex of the lobster were also included as additional fixed effects, and lobster ID was included as a subject level random effect. Distance to attraction followed a log-normal distribution and was transformed prior to analysis. Linear mixed models were built using the R library nlme (Pinheiro et al., 2015), nested models were estimated using maximum likelihood and compared using likelihood ratio tests.

Three null models, based on each post-trap trajectory, were built using AdehabitatLT (Calenge, 2006). Null models either randomised the turn angle, the step length, or both the turn angle and the step length. Null models had the same number of positions and the same fixed start point as the observed post-trap trajectory. The first alternate hypothesis was that the minimum distance between lobsters and a baited trap was less than would be expected by chance. The minimum distance between the lobster and the approached trap was calculated for each null trajectory and permutation tests were used to investigate non-random movement towards a trap. Models were run 999 times, if the result of the permutation test was $p \leq 0.05$ the model was run again for 99999 times and an updated p value derived. The second alternative hypothesis was that the number of observed lobster detections within 20 m would be greater than expected by chance, this was tested in an identical way to the first.

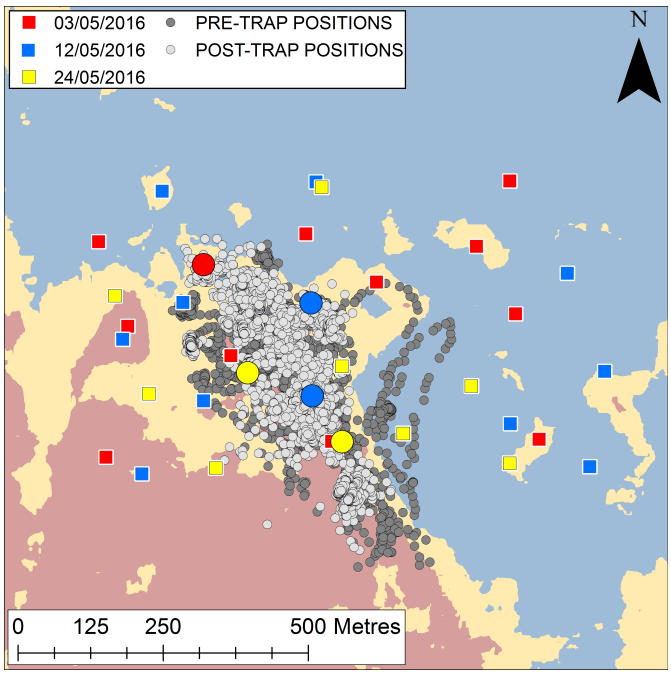

Figure 2.3: Pre and post-trap lobster positions in relation to traps. Red squares = trap deployment 1 on the 3rd of May, blue squares = trap deployment 2 on the 12th of May, yellow squares = trap deployment 3 on 24th of May. Traps that were approached are represented by circles coloured to correspond with their deployment date. Hard substrate = red, mixed substrate = yellow, soft substrate = blue.

2.3 Results

Twelve of the fourteen tagged lobsters were successfully recorded within the study site during the pre-trap period and eleven were detected during the post-trap period. Six of the remaining eleven lobsters were detected within 20 m of a baited trap. The number of detections for these six lobsters ranged from n = 383 (lobster 28187) to n = 1638 (lobster 28179) in the pre-trap period and from n = 81 (lobster 28192) to n = 235 (lobster 28179) in the post-trap period. Lobster 56815 was detected within 20 m of two traps, one during the 2nd deployment and one during the 3rd deployment. The mean error $\pm$ 1 s.e. associated with post-trap data ranged from 7.36 m $\pm$ 0.20 (lobster 28192, n = 81) to 8.84 m $\pm$ 0.25 (lobster 28187, n = 103). Five lobsters did not move within 20 m of a trap during any of the deployment periods and twenty-nine of the thirty-four traps were not visited, and are not considered further.

2.3.1 Behaviour and movement in the presence and absence of traps

All the traps that were approached were located on 'mixed' or 'hard' substrate (range 69.30 - 91.50), reflecting lobster movements during the pre-trap period (Fig. 2.3). Of the twenty-seven visits within 20 m of the approached traps sixteen were initiated between 2000 h and 0600 h (Table 2.1). There were seven periods where lobsters were detected within 20 m of the traps for 5 h or more, five of these occurred after 0600 h

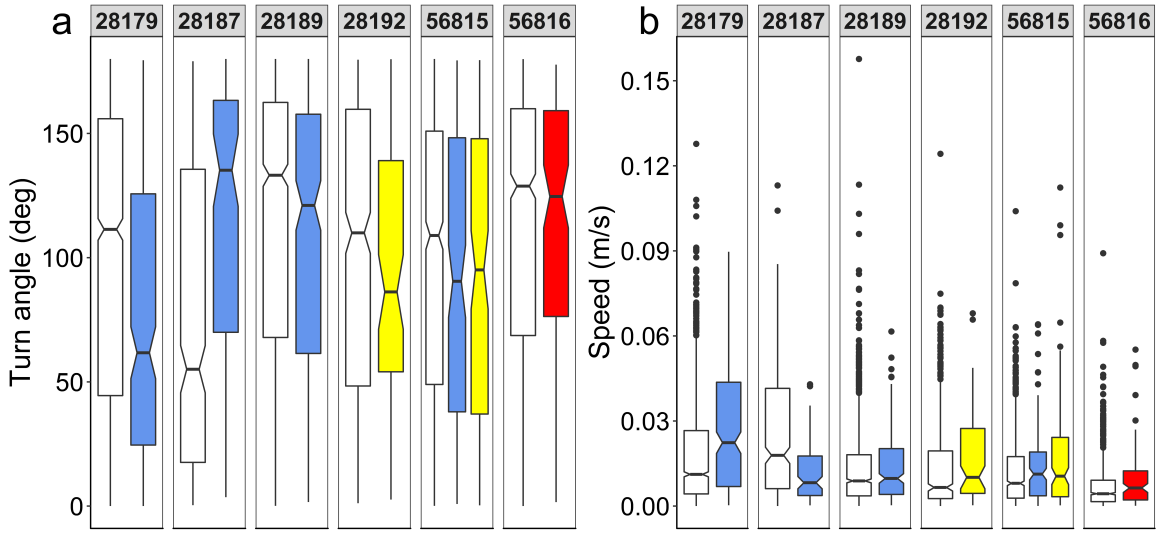

Figure 2.4: Comparison of lobster movement metrics. a) Turn angle, b) speed. White = pre-trap, red = 1st deployment, blue = 2nd deployment, yellow = 3rd deployment. Numbers above plots correspond to individual lobsters. Boxes = interquartile range (IQR), notches = 95% confidence intervals for the median (horizontal line), and whiskers = 1.5*IQR.

(Table 2.1). Duration ranged from 3 min to 16 h 55 min (lobster 28192 and lobster 28187, respectively). The minimum distance to the trap during these periods ranged from 1.03 m to 17.93 m (lobster 56816 and lobster 28187, respectively); two occurred within 12 h of the trap deployment (2.82 m, lobster 28179 & 1.03 m, lobster 56816), a further one occurred within 24 h (9.47 m 56815, 3rd deployment), and another occurred within 48 h (9.68 m, 28192) (Table 2.1).

There was no clear overall pattern in turn angle (Fig. 2.4a) or speed (Fig. 2.4b) between pre and post trap periods as there was considerable individual variation (Fig. 2.5). Three lobsters exhibited a lower median turn angle and higher median speed during the post-trap period (lobsters 28179, 56815, and 28192, Fig. 2.4 a, Fig. 2.4 b), and two only exhibited a change in turn angle or speed (lobsters 28189 & 56816, Fig. 2.4 a, Fig. 2.4 b). Lobster 28187 exhibited higher median turn angles, and lower median speeds during the post-trap period (Fig. 2.4 a, Fig. 2.4 b). There was evidence of overlapping space use during the post-trap period (lobster 28187, Fig. 2.5 b & lobster 28189, Fig. 2.5 c). Only two lobsters used space during the post-trap period that they had not used during the pre-trap period (56815, Fig. 2.5 e & 28192, Fig. 2.5 f).

2.3.2 Movement in response to a bait source

Lobster movements towards traps in relation to the current direction were investigated for five of the six lobsters (Table 2.2); the approach by lobster 56816 occurred during the 1st deployment and could not be assessed as the current meter was only deployed from the 2nd deployment onward. The current direction within the study site was north-south in orientation and current speed ranged from

0.001 - 0.415 ms^{-1}.

Eighteen of the twenty-two turns towards the trap, regardless of turn angle, occurred between 2000 h and 0600 h, ten approaches occurred within the first 24 h of deployment. Four turns resulted in movement against the current, only lobster 28179 made more than one turn against the current (Table 2.2). Four lobsters made multiple turns towards their approached trap (Table 2.2). The time lobsters spent within 20 m of the trap after an approach varied considerably (3 min lobster 28192 - 10 h 20 min lobster 28179, Table 2.1 and Table 2.2). Lobster 28192 was only detected once within 20 m of the trap on its first approach (Table 2.2), and therefore time spent within 20 m could not be estimated for inclusion in Table 2.1.

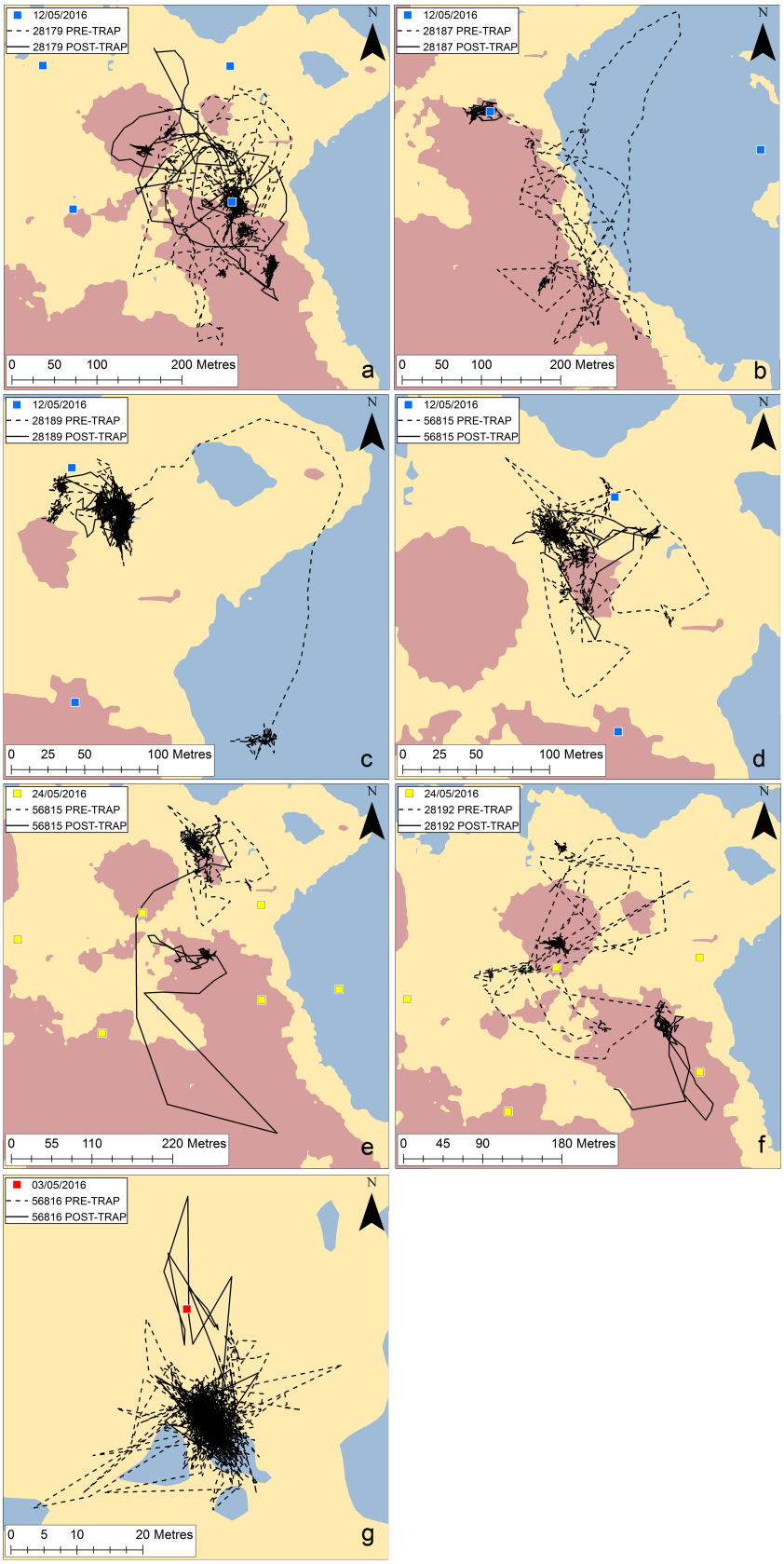

Figure 2.5: Movement in the absence and presence of traps. a) lobster 28179, b) lobster 28187, c) lobster 28189, d) lobster 56815 deployment 2, e) lobster 56815 deployment 3, f) lobster 28192, g) lobster 56816. Pre-trap trajectories = black dashed line, post-trap trajectories = solid line. Coloured squares represent traps deployed at the time of approach.

Table 2.1: Continuous time periods within 20 m of the approached trap. Duration calculated as the time difference between the first and last detection within 20 m. [a] denotes periods that have resulted from an approach specified in Table 2.2.

Tag ID	Start Time Date	End Time Date	Duration (hours) (*n* Detections)	Minimum Distance (m)
28179	10:19 12-05	20:39 12-05	10.33 (45)	2.82[a]
28179	00:54 13-05	01:04 13-05	0.17 (3)	9.14[a]
28179	01:08 14-05	01:25 14-05	0.28 (4)	5.31[a]
28179	22:11 14-05	22:21 14-05	0.17 (2)	16.81[a]
28179	22:49 14-05	22:53 14-05	0.07 (2)	17.93[a]
28187	22:56 12-05	02:16 13-05	3.33 (5)	5.31
28187	03:28 13-05	20:24 13-05	16.93 (2)	6.37
28187	22:37 13-05	09:45 14-05	11.13 (6)	4.55
28187	16:50 14-05	00:21 15-05	7.52 (18)	2.28[a]
28187	02:56 15-05	03:00 15-05	0.07 (2)	17.66
28187	03:40 15-05	09:24 15-05	5.73 (11)	2.65[a]
28189	12:41 14-05	13:27 14-05	0.77 (5)	8.68[a]
28192	21:52 25-05	21:55 25-05	0.05 (2)	9.68[a]
56815	23:36 14-05	00:11 15-05	0.58 (3)	15.62[a]
56815	07:46 25-05	07:52 25-05	0.10 (2)	9.47[a]
56816	20:07 03-05	21:19 03-05	1.20 (8)	11.32
56816	21:40 03-05	22:01 03-05	0.35 (5)	11.73
56816	22:18 03-05	02:28 04-05	4.17 (21)	1.03[a]
56816	02:50 04-05	03:07 04-05	0.28 (3)	11.22[a]
56816	03:51 04-05	04:49 04-05	0.97 (5)	17.25
56816	05:27 04-05	05:55 04-05	0.47 (4)	17.25
56816	08:18 04-05	08:33 04-05	0.25 (4)	13.77
56816	09:04 04-05	10:04 04-05	1.00 (9)	13.74
56816	10:16 04-05	18:01 04-05	7.75 (6)	10.85
56816	19:02 04-05	22:22 04-05	3.33 (14)	12.16
56816	03:51 05-05	05:11 05-05	1.33 (2)	13.06
56816	06:16 05-05	12:06 05-05	5.83 (9)	11.22

Table 2.2: Trap approaches resulting from turns greater than 30°. DA = distance of attraction, Time = time the approach began, Soak time = complete hours since trap deployment, and Minimum distance = minimum distance between the lobster and the trap. Speed change indicates if the speed of the lobster increased ↗ or decreased ↘ as it arrived at the trap.

Tag ID	DA (m)	Time	Soak time (Deployment)	Relative angle (deg)	Current speed (ms^{-1})	Min. dist. (m)	Speed change
28179	16.35	14:41	4 h (2)	88.31	0.05	8.49	↗
28179	14.17	15:07	5 h (2)	120.35	0.05	9.33	↗
28179	15.35	15:20	5 h (2)	66.07	0.09	2.82	↘
28179	58.37	00:41	15 h (2)	263.19	0.11	9.14	↘
28179	125.55	00:09	38 h (2)	187.69	0.07	5.31	↘
28179	48.87	22:00	59 h (2)	198.33	0.14	16.81	↗
28179	34.27	22:34	60 h (2)	89.41	0.09	17.93	↗
28187	27.99	02:28	16 h (2)	254.09	0.05	6.37	↗
28187	10.27	22:37	36 h (2)	84.79	0.08	7.76	↘
28187	9.03	23:45	37 h (2)	89.53	0.03	5.09	↗
28187	14.68	01:04	38 h (2)	214.325	0.07	4.55	↘
28187	13.40	20:07	58 h (2)	31.49	0.09	2.28	↗
28187	7.57	03:40	65 h (2)	279.87	0.11	2.65	↗
28189	28.64	08:13	45 h (2)	154.85	0.13	8.68	↘
28192	32.68	20:22	34 h (3)	174.13	0.05	12.60	↘
28192	39.25	21:34	35 h (3)	56.30	0.15	9.68	↘
56815	46.48	23:13	60 h (2)	52.63	0.12	15.62	↘
56815	114.64	03:40	17 h (3)	34.53	0.21	9.47	↗
56816	5.40	22:37	10 h (1)	-	-	1.03	↘
56816	6.70	23:20	10 h (1)	-	-	3.14	↗
56816	5.66	00:41	11 h (1)	-	-	3.06	↘
56816	14.74	02:50	14 h (1)	-	-	11.22	↗

The mean distance of attraction for all turns greater than 30°, regardless of current direction, was 31.37 m ± 6.94 s.e., n = 22, and the mean distance of attraction for approaches that occurred within the first 24 h was 27.94 m ± 10.83 s.e., n = 10. The mean distance of attraction for turns toward the trap greater than 30° that resulted in movement against the current was 58.94 m ± 22.63 s.e., n = 4. Trap approach speeds varied between individuals. Twelve of the twenty-two trap approaches (Table 2.2) resulted in a decrease in speed immediately before arriving at the trap. The initial linear mixed model contained only the subject level random effect and accounted for 46.53 % of the variation within the distance of attraction. The model including current speed as a covariate was significantly better when compared to the random effect only model (χ^2= 3.89, d.f. = 1, p = 0.049), however current speed was not a significant covariate in this model (p = 0.070). The inclusion of additional fixed effects, time since trap deployment (χ^2= 0.16, d.f. = 1, p = 0.688), and sex of lobster (χ^2= 1.02, d.f. = 1, p = 0.314), did not significantly improve the model fit when compared to the model containing both current speed and the subject-level random effect. There was insufficient data to investigate the relationship using only turns that resulted in movement against the current.

2.3.3 Null models

Only lobster 56815 (3rd deployment) was closer to the approached trap than would be expected under random movement for all three null models, turn angle only (X = 9.47, E = 70.47, p = 0.027), turn and step length (X = 9.47, E = 74.57, p = 0.038) and step length only (X = 9.47, E = 76.95, p = 0.035). Three lobsters had a significantly greater number of positions less than, or equal to 20m from the approached trap than would be expected under random movement using null models generated from the post-trap trajectories (Table 2.3). The observed values were significantly greater than the expected values generated by all three null models for lobster 28179, turn angle (X = 56, E = 27.75, p = 0.025), turn angle and step length (X = 56, E = 7.59, $p < 0.001$), and step length (X = 56, E = 11.11, $p < 0.001$). The observed number of positions was only significantly greater than expected for lobster 56815 (3rd deployment) when compared to the null model that randomised the turn angle (X = 2, E = 0.307, p = 0.033). The observed number of positions for lobster 56816 was greater than expected when compared to the null model that randomised the turn angle (X = 92, E = 25.94, p = 0.015), and the turn angle and step length (X = 92, E = 28.18, p = 0.008). Two of the three lobsters (28179 and 56816) had a significantly greater number of positions, less than, or equal to, 20 m from the location of the trap when compared to null models based on the pre-trap trajectories ($p < 0.001$) (Table 2.4). The number of positions of lobster 56815 within or equal to 20 m was not significantly greater than would be expected under random movement when compared to null models generated from the pre-trap trajectory (X = 0, E = 5.68, p = 1.000).

Table 2.3: Results from null models (99999 permutations) generated from post-trap trajectories comparing the observed and expected number of positions $\leq$ 20m from the location of the approached trap.

Tag ID	Trap no. (Deployment)	Null model	Observed	Expected	Variance	Sim. p value
28179	2 (2)	Turn	56	27.75	154.33	p=0.025
28179	2 (2)	Turn & step	56	7.59	33.83	p<0.001
28179	2 (2)	Step	56	1 1.11	49.97	p<0.001
56815	3 (3)	Turn	2	0.307	5.88	p=0.033
56816	7 (1)	Turn	92	25.94	568.36	p=0.015
56816	7 (1)	Turn & step	92	28.18	521.825	p=0.008

Table 2.4: Results from null models (99999 permutations) generated from pre-trap trajectories comparing the observed and the expected number of positions $\leq$ 20m from the location of the approached trap.

Tag ID	Trap no. (Deployment no.)	Null model	Observed	Expected	Variance	Sim. p value
28179	2 (2)	Turn	574	31.39	773.06	p<0.001
28179	2 (2)	Turn & step	574	2.28	529.00	p<0.001
28179	2 (2)	Step	574	30.52	718.59	p<0.001
56815	3 (3)	Turn	0	5.68	274.41	p=1.000
56816	7 (1)	Turn	690	83.93	5588.50	p<0.001
56816	7 (1)	Turn & step	690	71.37	4343.33	p<0.001

2.4 Discussion

This is the first study investigating free-ranging *H. gammarus* movements in response to baited traps. Although the number of tagged lobsters was small, six of the twelve successfully tagged lobsters appeared to respond to the baited traps, a similar proportion to a previous study (Watson III et al., 2009). However, five lobsters did not move within 20 m of a trap during any of the three deployments. It was not possible to infer the reason for this, but it does underline the role of individual variation in influencing a response to a bait source (Zimmer-Faust, 1989; Karnofsky and Price, 1989a), and the possibility that not all individuals within a population are equally available to the fishery. The equal sampling of individuals by a fishery is an assumption of assessment models, and a key source of uncertainty (Bannister and Addison, 1986; Smith and Addison, 2003; Maunder et al., 2006).

2.4.1 Behaviour and movement in the presence and absence of traps

There was no clear overall change in movement or behaviour when the pre-trap period was compared to the post-trap period, although there were differences between individuals. There was evidence of more directional movements characterised by lower median turn angle and higher median speed in the post-trap period for four lobsters, and one lobster exhibited more restricted and tortuous movements reflected in a higher median turn angle and lower median speed. The remaining lobster showed no difference in movement patterns between the pre-trap and post-trap period. Attributing behavioural change to the presence of a trap is difficult as changes in behaviour associated with the presence of a trap are unlikely to be maintained for the duration of a deployment. However, the scale of the movements undertaken in the post-trap period by lobsters 28189 and 56815 (2^{nd} deployment) was distinctly different from the pre-trap period.

Daytime trap approaches have previously constituted 33 % of all trap approaches (Watson III et al., 2009). It is therefore plausible that the lobsters remained at the location because of a trap, particularly as three of the four prolonged periods (greater than 5 h) occurred within 24 h of trap deployment. The time spent within 20 m of a trap in this study ranged from 3 min to almost 17 h, similar to previous studies (10 min and 12 h (Skajaa et al., 1998; Watson III et al., 2009)). However, direct comparisons are difficult due to the differing definitions of an approach (Skajaa et al., 1998; Watson III et al., 2009).

2.4.2 Movement in response to a bait source

Eighteen of the twenty-two approaches in this study occurred between 2000 h and 0600 h reflecting the low daytime activity levels of *H gammarus* (Smith et al., 1998c, 1999, 2000). *H. americanus* (Watson III et al., 2009) and *C. pagurus* (Skajaa et al., 1998), are more likely to approach traps at night, but there is no recorded relationship between the time of day and the probability of *H. americanus* entering a trap (Jury et al., 2001).

There were four turns greater than 30° that also coincided with movement against the current. Approaches that did not result in movement against the current may be return journeys to previously known areas (Karnofsky et al., 1989a; Jernakoff and Phillips, 1988). The second approach by lobster 28192 did not result in movement against the current and it is possible that it navigated back to the trap location known from its previous visit. Other turns that did not result in movement against the current should not be immediately discounted. Lobsters can be lured from their shelters by the presence of traps (Karnofsky and Price, 1989a) and it is feasible that a lobster in close proximity to the trap soon after deployment, such as lobster 28179, could have been influenced by a diffuse odour, or the presence of other lobsters. Likewise the turn towards the trap by lobster 56815 during the 3rd deployment was not against the current, but subsequent detections did result in movement against the current. These less obvious changes in direction made it difficult to decide when a lobster first became 'aware' of a trap and truly began its approach. It is unclear from this small study if identifying a strong directional change is the best arbiter of behavioural change. An increase in speed (Skajaa et al., 1998) may provide an alternative indicator. Just over half of the trap approaches in this study resulted in an decrease in speed at the trap. A decrease in speed has been previously reported for aquarium *H. americanus* (Moore et al., 1991). However, in a mesocosm study no change in speed on approach was reported (Watson III et al., 2009). In a free-ranging study a lobster could change speed due to terrain or behavioural interactions and more experimental work is necessary before speed can confidently be related to trap approach.

Previous studies (Jury et al., 2001; Watson III et al., 2009) have discounted approaches by lobsters that have appeared to 'walk past' traps. Lobsters can fail to approach, or leave the vicinity of a trap, in response to the presence of a more dominant animal and exhibit caution when approaching (Karnofsky and Price, 1989a), (Miller, 1980, crabs), (Bjordal, 1986, *Nephrops*). As the behaviour of lobsters in this study could not be observed, all approaches were considered. A trap mounted camera (Jury et al., 2001; Watson III et al., 2009) could not be used to validate approaches in this study; lobster locations were not known prior to trap deployment, and a location for such a system could not have been prioritised. To minimise uncertainty, data were restricted

to the 72 h after deployment and greater confidence should be associated with approaches that occurred within the first 24 h (Bennett, 1974).

There was a marginal relationship between distance of attraction and current speed. The number of approaches was small, and it is unlikely that the single current meter was able to adequately capture the fine scale changes in the current that would be experienced by the lobsters' olfactory system. The directional current could explain the large mean distance of attractions, almost three to five times larger than previously observed for *H. americanus* (Watson III et al., 2009). The directional current meant that an assumption of a circular plume (Watson III et al., 2009) would have been unrealistic. As the shape of the bait plume was not known the distance of attraction could not be converted into an estimate of area of bait influence. However, it should not be assumed that a larger distance of attraction would result in a larger area of bait influence, the 'effective trapping area' may actually be smaller under strong current conditions due to dilution (McQuinn et al., 1988). Although this would likely be compounded by reduced movement of lobsters under increased current speeds (Howard and Nunny, 1983). It is difficult to draw direct comparisons between experimental studies and free-ranging lobsters. It is likely that mesocosms and aquariums restrict movement and indirectly inflate the number of approaches (Karnofsky and Price, 1989a), or restrict the maximum distance of attraction (Watson III et al., 2009). The selection of more sedentary lobsters may also have created a bias that resulted in a reduced distance of attraction (Watson III et al., 2009). Approaches by free-ranging lobsters that have originated down current of traps have been initiated at distances of 42 m (Skajaa et al., 1998, *C. pagurus*) and 120 m (Jernakoff and Phillips, 1988, *Panulirus cygnus*). Due to the close initial proximity of lobsters 28179 and 56816 to traps it was sometimes difficult to differentiate general movement from a genuine approach in a small number of cases; this could have potentially biased the results towards longer approach distances.

2.4.3 Null models

Null models were used to investigate two aspects of trap proximity. Firstly, that the minimum distance to the trap during the observed trajectory was less than would be expected under random movement, and secondly, that the number of detections within 20 m of the trap was greater during the observed trajectory, than would be expected under random movement. Three lobsters had a greater number of post-trap positions within 20 m of the approached trap than would be expected under random movement, however two of those three also had a greater number of pre-trap positions within 20 m of the intended trap location, than would be expected under random movement. This suggests that both lobster 28179 and lobster 56816 had a previously established association with the trap location, such as a pre-existing shelter

or known foraging area. The minimum distances between lobsters and the approached traps were also not significantly different from random for four of the five lobsters. A pre-existing non-random association with a trap location, will likely increase the time spent near the trap, and reduce the minimum distance from the trap. However it is unclear if this proximity translates into increased probability of capture. Lobsters that exhibit wider ranging movement, such as lobster 56815, may encounter more traps than a comparatively sedentary lobster. If however the sedentary lobster is within a heavily fished area, it may have a higher probability of capture. Movement has been positively correlated with catchability for *H. americanus* due to the increased energy expenditure associated with seasonal dispersal (Bowlby et al., 2007). However movements by *H. gammarus* are generally smaller in scale, and although possible, there is no definitive evidence that resident or dispersal movement states occur (Moland et al., 2011b,a; Smith et al., 1999). So while increased mobility might result in greater trap exposure (Wiig et al., 2013) it is not clear whether the energetic demands of more localised short-term movements would be sufficient to create a similar relationship between movement and catch. If movement patterns were to differ between life-histories a relationship between movement and catch could have considerable management implications.

Null trajectories were not constrained to a specific range of substrates and simulated lobsters were able to move freely depending on the randomisation of the turn angle and, or step length. This reflected lobster movement during the pre-trap period of this study, and lobster movement from an adjacent study area of similar substrate composition (Skerritt et al., 2015). However, it is possible that lobster movements were constrained by other factors that were not accounted for in the models such as, the direction of the current (Howard and Nunny, 1983) or the distance from a known defensible shelter (Karnofsky et al., 1989a).

2.5 Conclusion

The aim of this study was to investigate the behaviour of free-ranging *H. gammarus* movements in response to spatially-explicit bait sources, and it is the first to do so. There were no consistent movement patterns between the pre and post trap period, although individual movement patterns did vary. The sample size of this study was small and further estimates of the distance of attraction for free-ranging lobsters are required to describe and understand the full range of behaviours. Acoustic telemetry studies, both observational and experimental, can provide important behavioural information on inshore fisheries species that could improve the estimates of CPUE. However, future experimental approaches are likely to still involve trade-offs between capturing the realism of the system, and controlling for confounding effects. A particular drawback to future free-range studies will be the small number of

approaches and the large number of traps that do not elicit a response. Large sample sizes and longer deployment periods, at increased expense, will be required to overcome this. If the distance at which a target species is under the influence of a bait plume is underestimated it could lead to an inaccurate estimate of both the area of bait influence, and the effective trapping area. Despite the uncertainty associated with free-range studies, the ability of lobsters to move freely underlines the variability of ranging behaviours, and the likelihood that attraction, and therefore catchability is not equal between individuals.

Earth, what a planet! On Earth, you enjoy eating a tasty clam. On my planet, clams enjoy eating a tasty you!

Dr Zoidberg

Chapter 3. Spatial overlap, space-sharing, and fine-scale behavioural interactions between pairs of European lobsters

3.1 Introduction

The degree of space sharing and behavioural interaction between individuals can have direct population consequences, influencing mate choice and availability (Hutchings et al., 1999; Van Der Meeren, 1994), avoidance of predators (Croft et al., 2009), transmissible diseases (Behringer et al., 2006), and access to potentially limited resources affecting survival, such as food (Moland et al., 2011b), and or shelter (Karnofsky et al., 1989a). These population level consequences determine the social and spatial structure of species and can be of great importance to management decisions (Carr et al., 2003; Hooker et al., 2011; Howarth et al., 2016). However, many commercially important marine species remain poorly studied in this respect. The wide availability of animal tracking devices in recent years, e.g. GPS, Argos, proximity loggers, and acoustic telemetry, have revolutionised how animal movement is studied, providing high-resolution data from which biologically meaningful behaviours can be inferred (Morales et al., 2004). These advancements are particularly marked for species that have been considered difficult to study, where continued miniaturisation and improved battery life have transformed data collection.

Homarus lobsters undertake a number of social behaviours, including dominance interactions (Skog et al., 2009) that are characterised by a wide range of avoidance and aggression behaviours (Scrivener, 1971; Atema and Cobb, 1980; Atema and Voigt, 1995). European lobsters *Homarus gammarus* are commercially valuable throughout their range; UK landings were worth £39.5 M in 2016 (Marine Management Organisation, 2017). Dominance interactions among *H. gammarus* and between *H. gammarus* and other species, such as *Cancer pagurus* can affect the probability of capture (Richards and Cobb, 1983; Miller and Addison, 1995; Addison, 1995; Watson and Jury, 2013). However, despite this commercial consequence, there has been little research on the occurrence of space-sharing or interaction in the field. The cryptic nature of *Homarus* spp. within the benthic environment makes studying their behaviour in the field challenging; previous behavioural observations have been made using SCUBA (Moland et al., 2011b; Cobb, 1971), or snorkelling (Karnofsky et al., 1989a). Acoustic telemetry provides an alternative methodology for collecting

high resolution data on animal movement remotely over long time periods, and without the expense or safety implication of repeated diver surveys. Previous acoustic telemetry studies on *H. gammarus* have focussed on space-use and home-range size (Wiig et al., 2013; Moland et al., 2011b; Skerritt et al., 2015), and have not addressed space-sharing, proximity, or interaction between individuals.

The availability of shelter providing habitat will likely determine the extent of space-sharing between *Homarus* spp. (Cobb, 1971; Howard, 1980; Bowlby et al., 2007), and subsequent possible interactions will be constrained by environmental conditions that determine lobster activity, such as seasonal changes in water temperature (Miller, 1990; Fogarty, 1988; Smith et al., 1998c, 2001, 1999; Robertson et al., 2016) and periodic variation in current speed (Moore et al., 1991; Moore and Atema, 1988; Howard and Nunny, 1983). The motivation of individuals to interact, and the length of subsequent interactions will be influenced by internal physiological states such as hunger regulation (Zimmer-Faust, 1989; Karnofsky and Price, 1989a), and in the case of interactions relating to reproduction and shelter sharing, the moult cycle (Tamm and Cobb, 1978).

Behavioural interactions among *Homarus* spp. are linked to the competition for shelters (Karnofsky et al., 1989a; Debuse et al., 2003). These interactions often result in the eviction of the resident individual (Karnofsky et al., 1989a; Karnofsky and Price, 1989b). Although lobsters' association with shelter weakens as they grow (Wahle and Steneck, 1992; Wahle, 1992a), they remain important in the avoidance of predators (Smith et al., 1998c) and unfavourable environmental conditions (Howard and Nunny, 1983). Shelters are also key to reproduction (Debuse et al., 2003) where shelters are shared between mated pairs during periods of mate guarding (Atema, 1986; Cowan and Atema, 1990). However, advanced courtship interactions between aquarium *H. gammarus* have taken place outside of shelters (Debuse et al., 2003). While this might indicate a behavioural or ecological difference between the two *Homarus* spp. (Debuse et al., 2003), the degree to which this behaviour occurs in the field under natural predation levels is unknown.

Chemical signalling via urine releases, as well as perceived differences in body size (Scrivener, 1971; Karnofsky et al., 1989a), mediate social interactions (Derby and Atema, 1982; Devine and Atema, 1982; Karavanich and Atema, 1998a; Skog, 2009a; Skog et al., 2009; Breithaupt et al., 1999). Although lobsters are less reliant on visual cues (Kaplan et al., 1993), they have been shown to visually recognise previous opponents in aquarium-based studies (Karavanich and Atema, 1998b; Gherardi et al., 2010). Urine releases by conspecifics are drawn back towards antennules by fanned appendages (Atema, 1995), and mate selection in the absence of visual cues has occurred at over 2 m in aquarium studies (Bushmann and Atema, 2000). It is unknown over what distance these chemical signals remain detectable in the field. *H.*

americanus can remember previous opponents for up to 24 h when no other individuals are present (Karavanich and Atema, 1998a). While the energetic benefits of avoiding repeated conflicts with a close neighbour are clear (Karavanich and Atema, 1993), the degree to which aggression is suppressed in the field will likely depend on lobster density and available habitat (Karnofsky and Price, 1989b). Aquarium and mesocosm studies are easily observable and can provide greater experimental control, but lack the realism of field studies and restrict movements (Watson III et al., 2009). Field studies on the behaviour and dominance of *H. americanus* suggest that high-level aggressive interactions between free-ranging lobsters may be lower than reported in laboratory studies as lobsters may occur at artificially high densities in tank experiments (Karnofsky and Price, 1989b; Karnofsky et al., 1989a). Although there are important considerations, such as the possible effect of tags on behaviour (Wilson and McMahon, 2006), and the logistical difficulty in 'ground-truthing' inferred behaviours, telemetry data are likely to provide a more biologically accurate assessment of lobster behaviour and interaction.

Interaction between individuals can be described as static if the interaction is quantified in terms of shared space only, or dynamic if it is quantified in terms of shared space and co-occurrence in time (Amlaner and Macdonald, 1980). Static interaction is typically measured using traditional home-range analysis such as kernel density estimation (Silverman, 1986) or minimum-convex polygon (Mohr, 1947) to quantify space use overlap (Millspaugh et al., 2004; Fieberg and Kochanny, 2005). As the performance of overlap indices can vary, consideration should be given to the purpose of the analysis when selecting an approach (Fieberg and Kochanny, 2005). For example, Bhattacharyya's affinity (BA) (Bhattacharyya, 1943) can reliably assess the similarity between utilization distribution (UD) estimates, and Utilization Distribution Overlap Index (UDOI) is particularly useful for assessing shared space-use (Fieberg and Kochanny, 2005).

Dynamic interaction can be assessed in terms of discrete data points known as 'point-based', such as proximity analysis (Prox) (Bertrand et al., 1996) and the spatial interaction method (IAB) developed by Benhamou et al. (2014), or as 'path-based' where sequential points form vectors of movement (Long and Nelson, 2013). Path-based approaches calculate step length and turning angle that are then compared to assess similarity in direction and displacement between individuals (Long and Nelson, 2013). *Homarus* spp. do not undertake cohesive movement in the same way that typically social animals would, for example marine mammals (Whitehead, 2016) or terrestrial herbivores (Michelena et al., 2010), and therefore point-based approaches are preferred over path-based. As the time between the detected positions of two co-occurring individuals is considered, it is possible to quantify the degree of relatedness (Amlaner and Macdonald, 1980), or interdependence (Doncaster, 1990), between the movements of paired individuals.

Movements with a high degree of relatedness, or interdependence are commonly termed attraction, and movements where individuals moving away from each other are termed avoidance, although the exact definition will depend on the index used (Long and Nelson, 2013; Benhamou et al., 2014; Shirabe, 2006). Several indices for quantifying dynamic interaction exist, but can vary in their effectiveness to identify biologically meaningful associations (Long et al., 2014; Miller, 2015) and care should be exercised when interpreting analyses.

The proximity of tagged individuals can be evaluated using purpose built tags that detect other proximal tags (Drewe et al., 2012), or calculated post-hoc using standard telemetry data from two or more co-occurring individuals that fulfill both a temporal and distance threshold (Bertrand et al., 1996). Proximity analysis can then be used to quantify contact rates between individuals (Kjær et al., 2008; Bertrand et al., 1996; Schauber et al., 2007; Baker and Harris, 2000). IAB (Benhamou et al., 2014) calculates the statistical significance of an interaction, by comparing the observed interaction to expected values generated by temporally shifting observations. IAB considers the distance between a dyad, and also explicitly incorporates serial auto-correlation, which is not considered in other indices (DI Long and Nelson, 2013) (Cr, Shirabe, 2006). The coefficient of sociality (Cs, Poole, 1995) also calculates the statistical significance of a potential interaction; however, the error rate is lower in IAB and is equally likely between avoidance and attraction (Miller, 2015) whereas in Cs Type I errors are more likely to be associated with attraction interactions, and type II errors are more likely to be associated with avoidance interactions. Proximity analysis and IAB occur on a scale between 0 and 1 where values close to 0 are representative of avoidance and values closer to one are representative of attraction.

The aim of this study was to use a hierarchical approach to assess spatial overlap, contact rates, and interaction between lobsters in the absence of fishing activities. It was hypothesised that areas of shared space use would occur on preferred shelter providing substrate, and that there would be a diel pattern in the contact rates between individuals reflecting increased levels of lobster activity; BA and UDOI were used to assess shared-space use, and proximity analysis was used to quantify contact rates. It was further hypothesised that lobsters that share space would move non-independently of each other. Attraction or avoidance between pairs of lobsters was tested using IAB.

3.2 Methods

3.2.1 Study site and data collection

Data were collected using a Vemco Positioning System (AMIRIX Systems Inc., Halifax, Canada) deployed approximately 2 km off Blyth, Northumberland UK

(approx. 55°07′46″N, 1°26′89″W) between the 23rd April and 3rd June 2013 (Skerritt et al., 2015). Lobsters (n= 44, CL 65-98 mm, Skerritt et al., 2015) were tagged with V13 transmitters (minimum transmission delay of 5 min) and released in the study area within 10 min. Analyses were completed in R 3.4.1. (R Core Team, 2017) using packages *adehabitatLT* (Calenge, 2006) and *WildlifeDI* (Long et al., 2014). Only pairs of lobsters that experienced temporal overlap during tracking, and had been separately detected at least 100 times, were considered in the analysis. A dyad was defined as a pairing that had two or more simultaneous locations within the temporal threshold. A dyad was categorised as 'female' if both lobsters were female, and 'male' if both were male, and 'mixed' if one lobster was male and the other was female. Prior to analysis detections with high positional error were identified using linear regression between two measures of horizontal positioning error (HPE and HPEm) (Skerritt et al., 2015; Coates et al., 2013). The model was weighted by the number of HPEm observations per whole value of HPE. This was to account for the exponential decline in the number of observations as the value of the HPE increased. Observations with a HPE greater than 24 were removed, limiting the maximum error to approximately 10 m and the mean error to approximately 4 m. The first 48 h of tagging data were also removed prior to conducting the analyses to avoid including behaviour resulting from the tagging procedure.

The substrate within the study site was characterised using an Olex AS (www.olex.no) echosounder. Olex software provides a measure of relative hardness on a linear scale between 1 and 100, where 100 is no energy lost; higher values are therefore associated with more reflective materials such rock. Data were subsequently classified as, 'Soft' such as mud and sand < 20, 'Mixed' such as, mud and rock > 20 and < 35, and 'Hard' such as continuous rock > 35. It is not possible to infer habitat type using this method as substrate roughness is not measured (Elvenes et al., 2013); however these data are a broad indicator of substrate type and have been previously validated using drop-down cameras in the vicinity of the study site (Skerritt et al., 2015).

3.2.2 Static interaction and space use overlap

Lobster utilization distributions (UD) and the indices of overlap between UDs were calculated using the R library *adehabitatHR* (Calenge, 2006). The smoothing parameter h was standardized across all lobsters and was chosen to minimise the degree of under and over smoothing between lobster UD estimates (Kie et al., 2010): h = 5.5 m, grid = 300, extent = 0.1. A fixed smoothing parameter was chosen over least-squares cross-validation due to a large number of repeat locations (Hemson et al., 2005). A home-range was defined as the 95UD isopleth and the 50UD was defined as a core area of habitat use. Both BA and UDOI indices range from 0 (non-overlapping UDs) to 1 (identical overlapping UDs), however UDOI can be > 1 if the UDs are

non-uniformly distributed and have a high degree of overlap (Fieberg and Kochanny, 2005).

3.2.3 Proximity and contact rates

Proximity analysis (Bertrand et al., 1996) was used to assess the proportion of proximal positions between each dyad $\alpha\beta$ where α and β are the individual lobsters.

$$Prox = \frac{ST\alpha\beta}{T\alpha\beta} \tag{3.1}$$

where $ST\alpha\beta$ is the dyad positions that fulfill both the temporal t_c and spatial threshold d_c; $T\alpha\beta$ is the positions that only fulfill the temporal threshold t_c. Proximity was calculated using five different values of d_c, 1 m = d_c1, 5 m = d_c5, 10 m = d_c10, 15 m = d_c15, and 20 m = d_c20, and six different values of t_c, 10 min = t_c10, 20 min = t_c20, 30 min = t_c30, 40 min = t_c40, 50 min = t_c50, 60 min = t_c60. Proximity values did not vary noticeably across the values of t_c, although it did increase with d_c in most cases (Figure 3.1). Subsequently t_c was set at 20 min and d_c varied at 1 m, 5 m, and 10 m. These values reflect the general slow movement of lobsters (O'Grady et al., 2001), and the minimum transmission delay of the tags (5 min). They allowed for the possibility of missed detections, and d_c values were comparable to the estimated positional error of lobster locations. The distance at which a free-ranging lobster is able to detect the urine of a conspecific is unknown, but varies with aggression levels and is highest after eating (Breithaupt et al., 1999). Urine release is in the region of 1-3 ml/h or approximately 2 % of the body weight (Breithaupt et al., 1999). Due to the uncertainty at which lobsters were aware of each other d_c was limited to 10 m. This distance threshold also captured proximity relating to resource sharing, such as the proximity of lobsters to shelter providing habitat (Cobb, 1971). The locations of proximal contacts for each dyad with a proximity value > 0 were calculated as the mid-point between two simultaneous and proximal positions as determined by d_c and t_c.

3.2.4 Space sharing and interactions

Interactions between lobsters that shared space were investigated using IAB. The error rate of IAB has been shown to be low and unbiased (Miller, 2015), however a conservative hierarchical approach similar to Benhamou et al. (2014) was used to reduce the possibility of erroneous interactions. As such the number of significant interactions was calculated for dyads where Bhattacharrya's coefficient was ≥ 0.1 and ≥ 0.2 using increasing values of Δ and time t, where Δ is the critical distance of influence between two animals, i.e. the distance at which the behaviour is thought to occur (Long et al., 2014; Benhamou et al., 2014). The statistical significance of joint

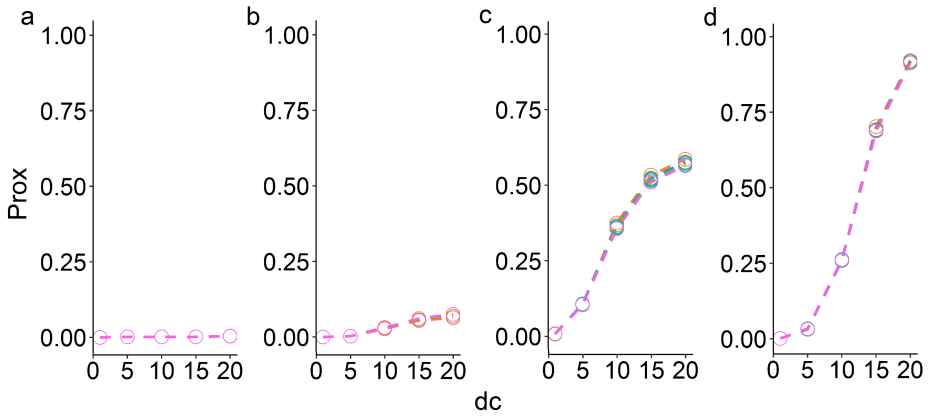

Figure 3.1: Changes in Prox values as d_c (metres) increases with different values of t_c (minutes) represented by different colour. a) no change Prox remains close to 0, b) marginal increase to maximum value of approximately 0.25, c) Prox increases with d_c to maximum value of approximately 0.5, d) sharp increase in Prox with d_c to at least 0.75. Red= 10 min, yellow = 20 min, green = 30 min, light blue = 40 min, dark blue = 50 min, and purple = 60 min.

movement can be assessed by comparing the observed to expected values via a permutation test, i.e. observed > expected = attraction, and observed < expected = avoidance (Benhamou et al., 2014). If dyads were only interacting for a short period of time due to one or both lobsters having several centres of activity the IAB analysis was repeated to examine only behaviour that occurred within the respective overlapping 95UD areas.

3.3 Results

Ten lobsters were excluded from the analyses; 3 lobsters were not detected within the study area, 6 lobsters had less than 100 detections over the course of the study, and 1 lobster had a malfunctioning tag. The remaining 34 lobsters (CL 65 - 92 mm, $\geq$ CL 87 mm, n = 4) were successfully tracked for between 25 days and 41 days (mean $\pm$ 1 s.e., 37.5 days $\pm$ 0.94, 16F and 18M). Damage and claw loss is common in commercial stocks (Scarratt, 1973); in this study 4 males were missing a claw (lobsters 160, 167, 213, and 216), 1 (lobster 210) had a damaged claw, and 1 female was regrowing a claw (lobster 198). There were 3 lobsters that were gravid at the time of tagging (lobsters 195, 204, and 209).

3.3.1 Space use and home range overlap

Female lobster home-ranges were consistently smaller than male home-ranges. The mean 95UD for females was 2068.35 $\pm$ 370.77 m^2, n = 16, compared to the mean male 95UD 6546.93 $\pm$ 1759.13 m^2, n = 18. Similarly female lobster 50UD core areas were also smaller, mean 319.44 $\pm$ 38.74 m^2, compared to male mean 50UD core areas 490.39 $\pm$ 65.59 m^2.

There were 36 dyads with overlapping 95UDs (BA $\geq$ 0.2), 25 of these dyads also had overlapping 50UD core areas (BA $>$ 0), (Table 3.1); BA and UDOI were highly correlated (r = 0.94). There were three mixed sex dyads where the 95UD had a UDOI $>$ 1, (Table 3.1). The home-range of male lobster 194 overlapped other home-ranges the most (n = 6 male dyads, and n = 3 mixed dyads). Male home-ranges overlapped other lobster home-ranges more than female home-ranges (male range 1-9 dyads, median 3 dyads, and female range 1-7 dyads, median 1 dyad). The majority of mixed dyads involved just three female lobsters, 163 (n = 6), 169 (n = 5), and 200 (n = 4). There were 6 lobsters that only overlapped as a female dyad, 2 lobsters that overlapped only as a male dyad, and 4 lobsters that only overlapped as a mixed dyad (3 females and 1 male) (Table 3.1).

The mean substrate hardness within areas of home-range overlap (95UD, BA $\geq$ 0.2) ranged from 20.34 $\pm$ 0.16 (167α 169β, n = 62) to 52.15 $\pm$ 0.25 (207α 216β, n = 74), (Fig. 3.2 and Fig. 3.3). The mean hardness of substrate within overlapping 50UD core areas (BA $\geq$ 0), which was likely to include lobster shelter habitat, ranged from 20.40 $\pm$ 0.30 (167α 169β, n = 8) to 53.96 $\pm$ 0.19 (167α 169β, n = 10) (Fig. 3.2 and Fig. 3.3). The mean substrate hardness of the overlapping areas of the 95UD and 50UD were $>$ 35, indicative of hard reef, for 3 of the 4 female dyads (mean 33.44 $\pm$ 6.12, n = 4, Fig. 3.2). The majority of the overlapping 95UD and 50UD areas between male dyads (n = 13), and between mixed dyads (n = 15) occurred on mixed substrate, (mean 24.07 $\pm$ 1.25 n = 15 Fig. 3.3a, and mean 26.81 $\pm$ 2.90, n = 17 Fig. 3.3b, respectively).

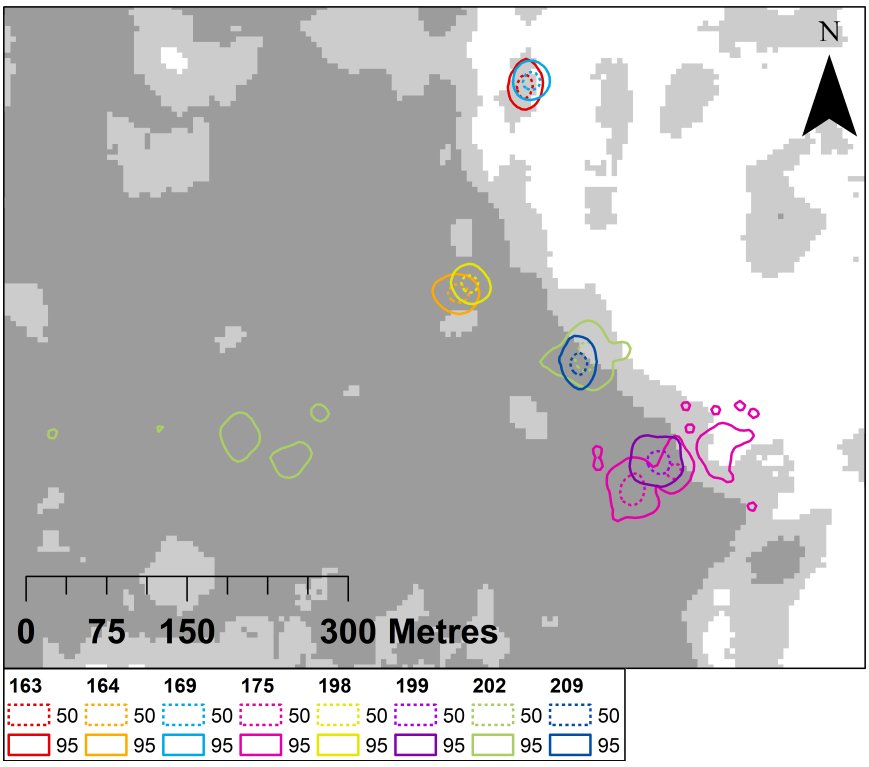

Figure 3.2: Overlap between female lobster home-ranges that had a BA $\geq$ 0.2. Unique numbers and colours in the legend refer to lobster IDs, and 50 and 95 refer to the 50UD (dashed line) and 95UD (solid line), respectively. Substrate map: white = soft substrate, medium grey = mixed substrate, and dark grey = hard substrate.

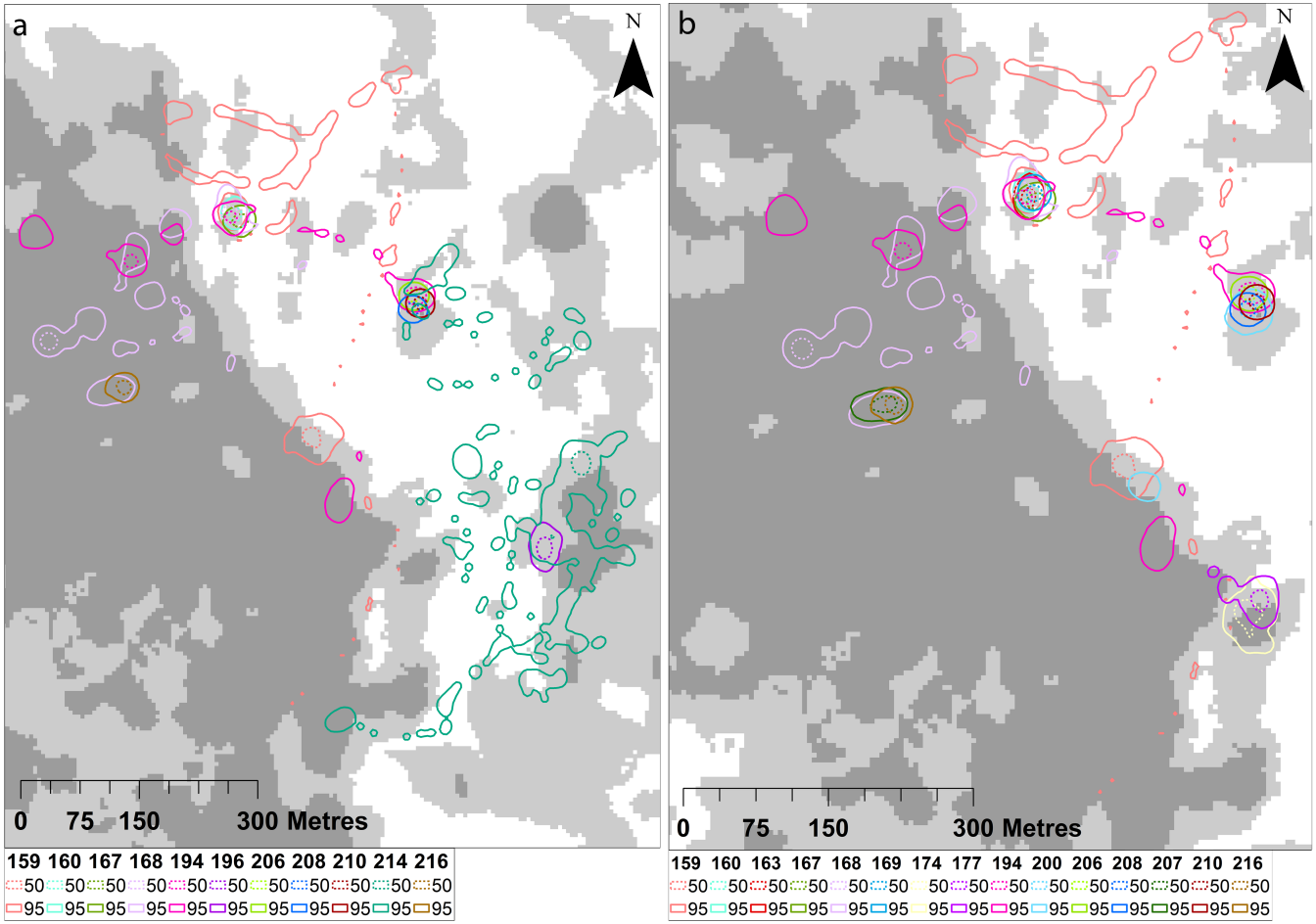

Figure 3.3: Overlap of lobster home-ranges that had a BA $\geq$ 0.2. Unique numbers in the legend and colours refer to lobster IDs, and 50 and 95 refer to the 50UD (dashed line) and 95UD (solid line), respectively. Substrate map: white = soft substrate, medium grey = mixed substrate, and dark grey = hard substrate. a) home-range overlap between male lobsters, b) home-range overlap between male and female lobsters.

Table 3.1: Spatial overlap between dyads when Bhattacharyya's coefficient (BA) $\geq$ 0.2. UDOI = Utilization Distribution Overlap Indices. Bold indicates BA 95UD $\geq$ 0.5 and/or UDOI 95UD $\geq$ 1.

Dyad $\alpha\beta$	BA 50UD	UDOI 50UD	BA 95UD	UDOI 95UD
Female				
163 169	0.216	0.047	**0.759**	0.801
164 198	0.030	0.001	0.444	0.244
175 199	0.000	0.000	0.279	0.107
202 209	0.234	0.056	**0.722**	0.886
Male				
159 160	0.000	0.000	0.252	0.109
160 167	0.154	0.024	**0.657**	0.594
160 168	0.192	0.039	0.480	0.413
160 194	0.092	0.009	0.334	0.190
167 168	0.054	0.003	0.328	0.174
167 194	0.026	0.001	0.269	0.110
168 194	0.100	0.010	0.277	0.206
168 216	0.000	0.000	0.215	0.069
194 206	0.302	0.097	**0.599**	0.679
194 208	0.000	0.000	0.206	0.060
194 210	0.127	0.017	0.413	0.276
196 214	0.000	0.000	0.269	0.113
206 208	0.000	0.000	0.331	0.138
206 210	0.067	0.005	**0.556**	0.414
208 210	0.070	0.005	**0.576**	0.437
Mixed				
159 163	0.000	0.000	0.236	0.090
159 169	0.000	0.000	0.209	0.064
160 163	0.361	0.132	**0.864**	**1.149**
160 169	0.342	0.119	**0.872**	**1.172**
163 167	0.190	0.037	**0.718**	0.731
163 168	0.206	0.044	0.485	0.431
163 194	0.120	0.015	0.361	0.224
167 169	0.198	0.040	**0.713**	0.691
168 169	0.088	0.008	0.368	0.210
168 207	0.000	0.000	0.274	0.115
169 194	0.029	0.001	0.277	0.121
174 177	0.027	0.001	**0.512**	0.377
194 200	0.000	0.000	0.220	0.076
200 206	0.000	0.000	0.334	0.152
200 208	0.413	0.176	**0.876**	**1.346**
200 210	0.131	0.017	**0.623**	0.612
207 216	0.228	0.053	**0.723**	0.746

3.3.2 Proximity and contact rates

Multiple individuals were involved in more than one dyad that resulted in 559 unique dyads with two or more simultaneous observations (t_c20). The number of dyads with Prox values > 0 (i.e. 1 or more observations that fulfilled both the temporal t_c and distance threshold d_c) reduced with d_c (Fig. 3.1 a-d), d_c10 = 45 dyads, d_c5 = 33 dyads, and d_c1 = 16 dyads. Dyad 200α 208β had the maximum Prox value for all combinations of d_c and t_c20 (0.71, 0.36, and 0.02, $T_{\alpha\beta}$ = 826) (Table 3.2). The minimum non-zero Prox value was ≤ 0.002 for all values of d_c. The decrease in Prox values followed 4 distinctive patterns, consistently low values of Prox for dyads that very infrequently fulfilled both the d_c and t_c thresholds (Fig. 3.1a), dyads that were occasionally proximal but only at higher values of d_c (Fig. 3.1b-c), or dyads that were proximal at all values of d_c, (Fig. 3.1d). There were 31 dyads that had overlapping 95UD and non-zero value for BA and a 0 value for Prox.

The difference in CL between paired individuals ranged between 0 mm and 33 mm (mean, 8.49 $\pm$ 0.28 mm), and the differences in CL between individuals were less at d_c1 compared to d_c10, (Table 3.3). The number of female dyads was similar at all values of d_c. The number of male only, and mixed sex dyads reduced at d_c1, (Table 3.2 and Table 3.3). The number of contacts per hour was highest between 1800 h and 0600 h regardless of d_c or the sex of paired individuals (Fig. 3.4a and b). Several lobsters were involved in more than one dyad, male lobsters had a higher median number of dyads than female lobsters and had the largest number of dyads at all values of d_c (10 = d_c10, 7 = d_c5, and 5 = d_c1, Fig. 3.4c).

Table 3.2: Proximity of dyads at decreasing values of d_c when BA $\geq$ 0.1. $n\ T_{\alpha\beta}$ is the number of simultaneous observations within t_c20.

Dyad $\alpha\beta$	BA95	$n\ T_{\alpha\beta}$	d_c10	d_c5	d_c1
Female					
163 169	0.759	504	0.494	0.111	0.004
202 209	0.722	98	0.327	0.082	0.010
164 198	0.444	230	0.148	0.013	0.004
175 199	0.279	66	0.015	0.000	0.000
Male					
160 167	0.657	750	0.348	0.085	0.001
194 206	0.599	673	0.361	0.220	0.021
160 168	0.480	456	0.368	0.107	0.009
208 210	0.576	752	0.259	0.032	0.001
206 210	0.556	657	0.204	0.029	0.002
194 210	0.413	352	0.105	0.009	0.000
159 160	0.252	524	0.082	0.025	0.002
160 194	0.334	339	0.080	0.029	0.000
167 168	0.328	407	0.079	0.022	0.000
168 216	0.215	67	0.075	0.000	0.000
196 214	0.269	222	0.050	0.014	0.000
159 168	0.148	328	0.049	0.012	0.000
167 194	0.269	350	0.031	0.003	0.000
206 208	0.331	733	0.029	0.003	0.000
194 208	0.206	394	0.010	0.000	0.000
168 213	0.121	517	0.008	0.002	0.002
159 167	0.148	554	0.007	0.000	0.000
168 194	0.277	283	0.004	0.000	0.000
Mixed					
200 208	0.876	826	0.713	0.361	0.023
160 163	0.864	268	0.646	0.261	0.019
160 169	0.872	1075	0.637	0.233	0.020
163 167	0.718	231	0.364	0.117	0.004
167 169	0.713	932	0.438	0.104	0.006
200 210	0.623	901	0.320	0.071	0.003
163 194	0.361	260	0.277	0.096	0.000
207 216	0.723	35	0.257	0.000	0.000
163 168	0.485	213	0.216	0.070	0.000
168 169	0.368	670	0.143	0.031	0.000
169 194	0.277	650	0.078	0.018	0.000
162 215	0.176	92	0.065	0.000	0.000
168 207	0.274	216	0.032	0.005	0.000
200 206	0.334	773	0.032	0.006	0.000
159 169	0.209	731	0.031	0.003	0.000
159 163	0.236	229	0.026	0.000	0.000
174 177	0.512	140	0.021	0.007	0.000
194 199	0.173	252	0.016	0.000	0.000
194 200	0.220	346	0.012	0.000	0.000
159 172	0.162	291	0.010	0.000	0.000

Table 3.3: The mean difference in CL between dyads that were proximal at differing values of d_c.

d_c	Female only	Male only	Mixed sex
10	5.50 ± 1.85 $n = 4$	6.37 ± 0.89 $n = 19$	8.23 ± 1.05 $n = 22$
5	5.33 ± 2.60 $n = 3$	5.80 ± 0.95 $n = 15$	8.47 ± 1.36 $n = 15$
1	5.33 ± 2.60 $n = 3$	4.86 ± 1.28 $n = 7$	7.50 ± 2.02 $n = 6$

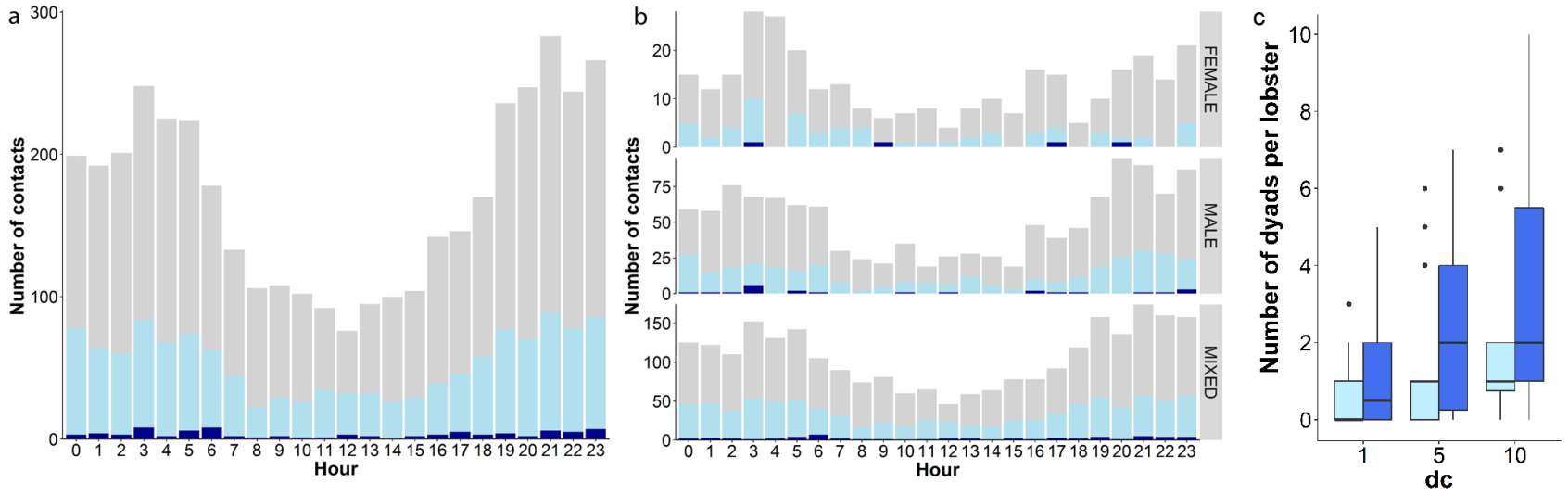

Figure 3.4: The number of contacts per hour as identified by proximity analysis (Prox), t_c = 20. a) all lobsters and b) contacts between female only, male only, and mixed sex dyads. Grey = d_c = 10 m, light blue = d_c = 5 m, dark blue = d_c = 1 m. c) The number of dyads per lobster, female = light blue, and male = dark blue.

3.3.3 Space sharing and interactions

The number of significant results identified by IAB increased with Δ, but did not vary with increasing values of t, or differ depending on whether BA = 0.1 or BA = 0.2 was set as the threshold for inclusion. As a result the more conservative threshold BA = 0.2 was used (Fig. 3.5); only significant interactions are reported (Table 3.4). There were 15 interactions when Δ = 10 m and all interactions were classed as an attraction. When Δ = 5 m there were 9 attraction interactions, and 6 avoidance interactions (Table 3.4). Two dyads that were classed as an attraction when Δ = 10 m changed to an avoidance when Δ = 5 m (Table 3.4). Subsequently an intermediate value of Δ = 7.5 m was used and resulted in $p > 0.50$ in both cases. The majority of male dyads exhibited avoidance when Δ = 5 m (Fig. 3.6 and Fig. 3.7). Three of these male dyads remained within approximately 50 m of each other throughout the tracking period, (Fig. 3.7). There were only 2 male dyads that had attraction interactions at Δ = 5 m (Table 3.4, and Fig. 3.6, 160α 168α and 194α 206α). The majority of mixed sex dyads had attraction at all values of Δ, only one had an avoidance at $\Delta \leq 7.5$ m (Table 3.4 and Fig. 3.8). There were several lobsters that interacted with more than one individual (Table 3.4) and some appeared to do so concurrently. For example, male lobsters 208 and 210 were attracted to female lobster 200, but avoided each other (Fig. 3.7 and Fig. 3.9). Similarly, male lobster 160 was attracted to female lobsters 163 and 169 (Fig. 3.10), and female lobster 169 was additionally attracted to male lobsters 167 and 168 (Fig. 3.9 and Fig. 3.8). The results from dyads that were reanalysed due to multiple areas of activity resulting in relatively short periods of interaction, relative to the total tracked period, were largely similar to those in Table 3.4, although observed values for both attraction and avoidance were larger (Table 3.5).

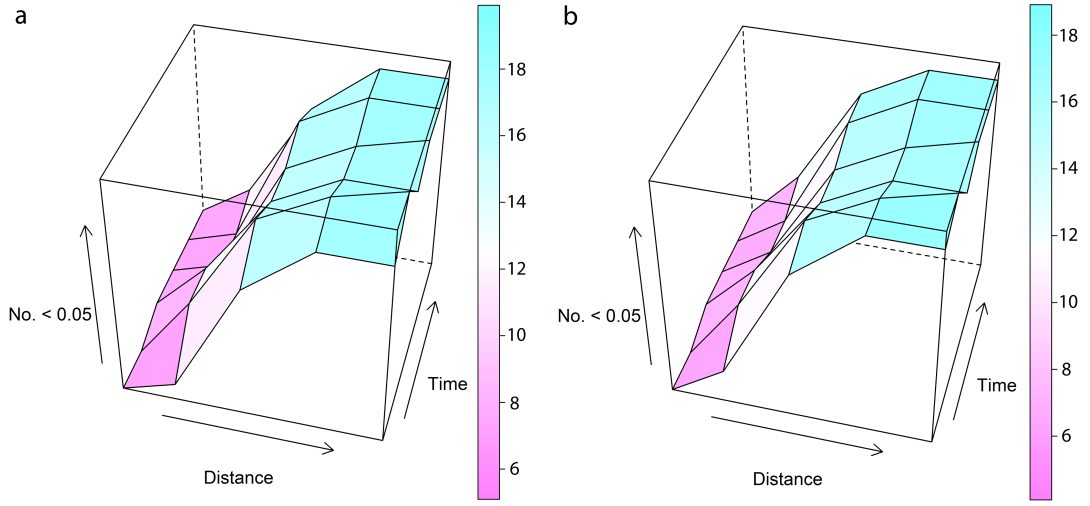

Figure 3.5: The number of significant attractions i.e. when observed interactions was larger than the expected when Δ is 1 m, 5 m, 10 m, 15 m, and 20 m, t increases at 10 min increments from 10 min to 60 min and a) Bhattacharyya's coefficient $\geq$ 0.1 or b) Bhattacharyya's coefficient $\geq$ 0.2

Table 3.4: Interaction between dyads where Bhattacharyya's coefficient was ≥ 0.2 for 95UD and where the observed interaction was significantly different from the expected interaction at t = 20 min. Blue text = attraction $p \leq 0.05$, red text = avoidance $p \leq 0.05$, black text = $p \geq 0.05$. [a] indicates dyads that were reanalysed and are presented in Table 3.5.

		Δ = 10 m			Δ = 7.5 m			Δ = 5 m		
Dyad $\alpha\beta$	n $T_{\alpha\beta}$	Observed	Expected	p	Observed	Expected	p	Observed	Expected	p
Female										
163 169	504	0.569	0.552	0.032	0.420	0.404	0.050	0.231	0.225	0.242
Male										
160 167	750	0.484	0.469	0.001	0.337	0.325	0.023	0.171	0.169	0.392
160 168[a]	456	0.382	0.345	0.002	0.296	0.256	0.002	0.177	0.143	0.002
160 194	339	0.082	0.071	0.041	0.066	0.054	0.038	0.042	0.033	0.068
194 206[a]	673	0.353	0.327	0.001	0.309	0.275	0.001	0.236	0.192	0.001
194 208[a]	394	0.114	0.116	0.168	0.045	0.050	0.020	0.006	0.009	0.003
194 210[a]	352	0.259	0.266	0.151	0.157	0.175	0.011	0.055	0.078	0.003
206 208	733	0.235	0.237	0.385	0.100	0.107	0.004	0.019	0.024	0.005
206 210	657	0.413	0.404	0.012	0.252	0.252	0.422	0.094	0.102	0.037
208 210	752	0.450	0.439	0.003	0.285	0.284	0.441	0.114	0.125	0.007
Mixed										
159 169[a]	731	0.046	0.051	0.082	0.031	0.037	0.041	0.013	0.020	0.007
160 163	268	0.661	0.612	0.004	0.534	0.481	0.004	0.353	0.305	0.007
160 169	1075	0.666	0.630	0.003	0.532	0.490	0.003	0.340	0.297	0.003
163 168	213	0.272	0.240	0.005	0.201	0.173	0.009	0.108	0.093	0.103
163 194[a]	260	0.264	0.232	0.008	0.219	0.181	0.012	0.146	0.112	0.035
167 169	932	0.541	0.519	0.001	0.391	0.370	0.001	0.207	0.195	0.031
168 169[a]	670	0.222	0.206	0.001	0.147	0.132	0.006	0.068	0.057	0.034
200 208[a]	826	0.685	0.646	0.001	0.587	0.535	0.001	0.427	0.365	0.001
200 210[a]	901	0.449	0.432	0.001	0.308	0.292	0.001	0.152	0.143	0.048

Table 3.5: Interaction between dyads using only observations that were within overlapping areas of their respective 95UDs where Bhattacharyya's coefficient was $\geq$ 0.2 for 95UD at t = 20 min. Blue text = attraction $p \leq 0.05$, red text = avoidance $p \leq 0.05$, black text = $p \geq 0.05$.

		Δ = 10 m			Δ = 7.5 m			Δ = 5 m		
Dyad $\alpha\beta$	n $T_{\alpha\beta}$	Observed	Expected	p	Observed	Expected	p	Observed	Expected	p
Male										
160 168	278	0.628	0.579	0.004	0.487	0.436	0.004	0.291	0.249	0.004
194 206	304	0.782	0.727	0.003	0.684	0.612	0.003	0.524	0.432	0.003
194 208	200	0.224	0.228	0.170	0.088	0.096	0.025	0.011	0.017	0.005
194 210	208	0.438	0.445	0.125	0.266	0.291	0.005	0.092	0.130	0.005
Mixed										
159 169	65	0.522	0.511	0.277	0.349	0.349	0.508	0.144	0.164	0.169
163 194	96	0.716	0.666	0.021	0.592	0.534	0.021	0.396	0.343	0.042
168 169	318	0.468	0.440	0.003	0.310	0.284	0.003	0.143	0.127	0.028
200 208	817	0.693	0.653	0.001	0.593	0.541	0.001	0.431	0.368	0.001
200 210	896	0.452	0.436	0.001	0.310	0.294	0.001	0.153	0.144	0.050

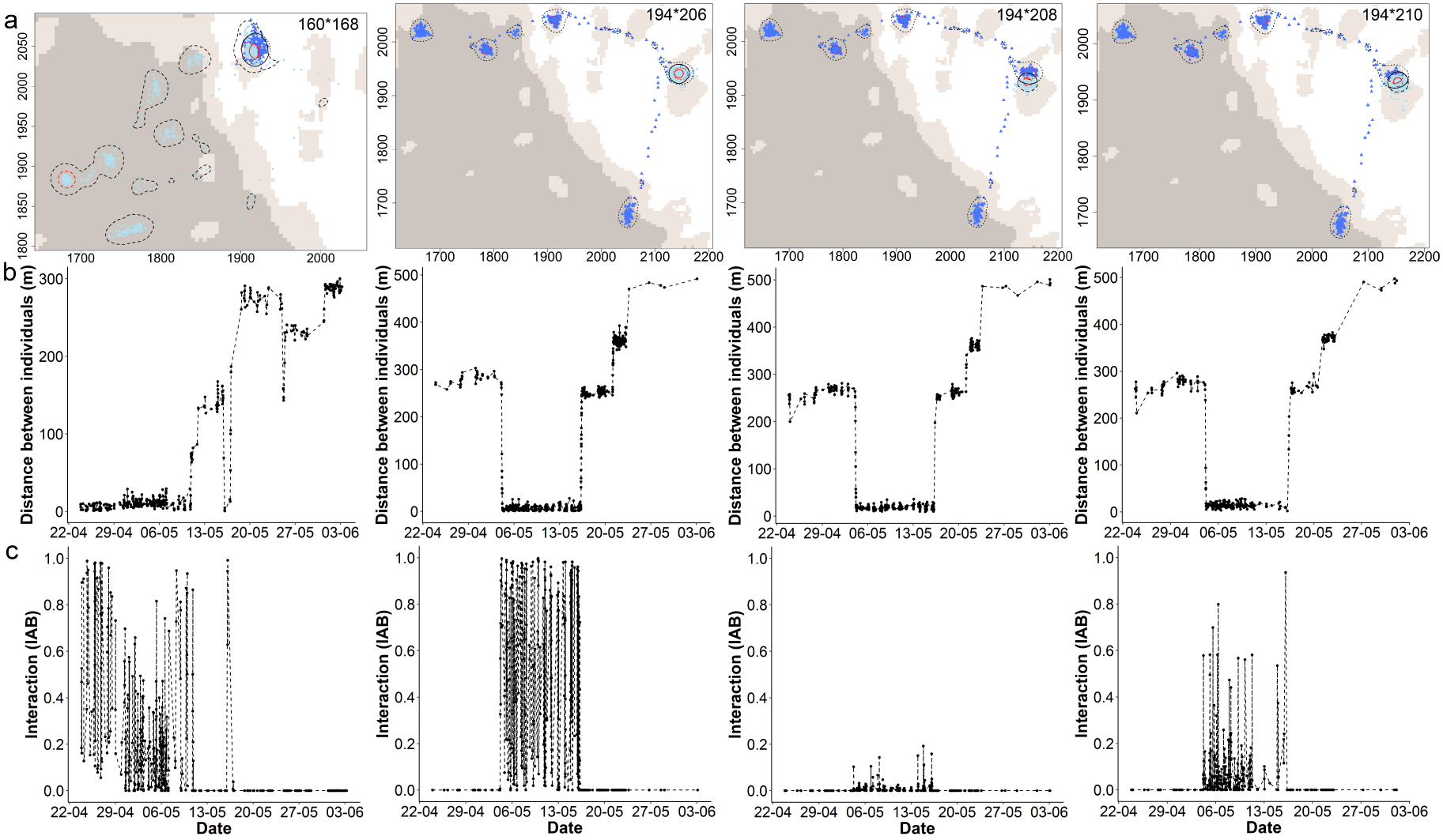

Figure 3.6: Movement and home-range overlap of male dyads $\alpha\beta$ where one individual has more than one centre of activity during tracking. a) dark blue points and dashed line = α, light blue points and dotted line = β, red line = 50UD and black line = 95UD, b) distance between dyad, and c) interaction index over time.

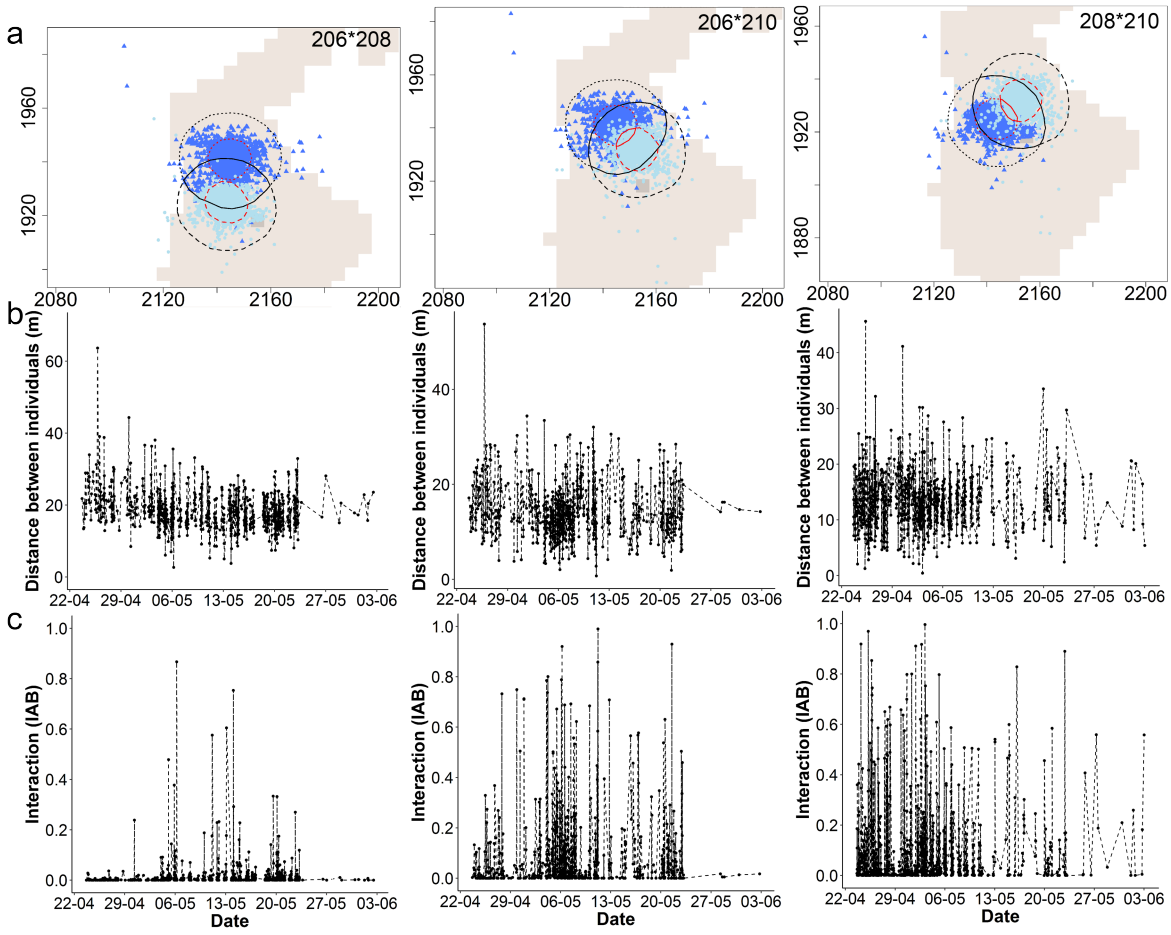

Figure 3.7: Movement and home-range overlap of male dyads $\alpha\beta$ that exhibited limited movement during tracking. a) dark blue points and dashed line = α, light blue points and dotted line = β, red line = 50UD and black line = 95UD, b) distance between dyad, and c) interaction index over time.

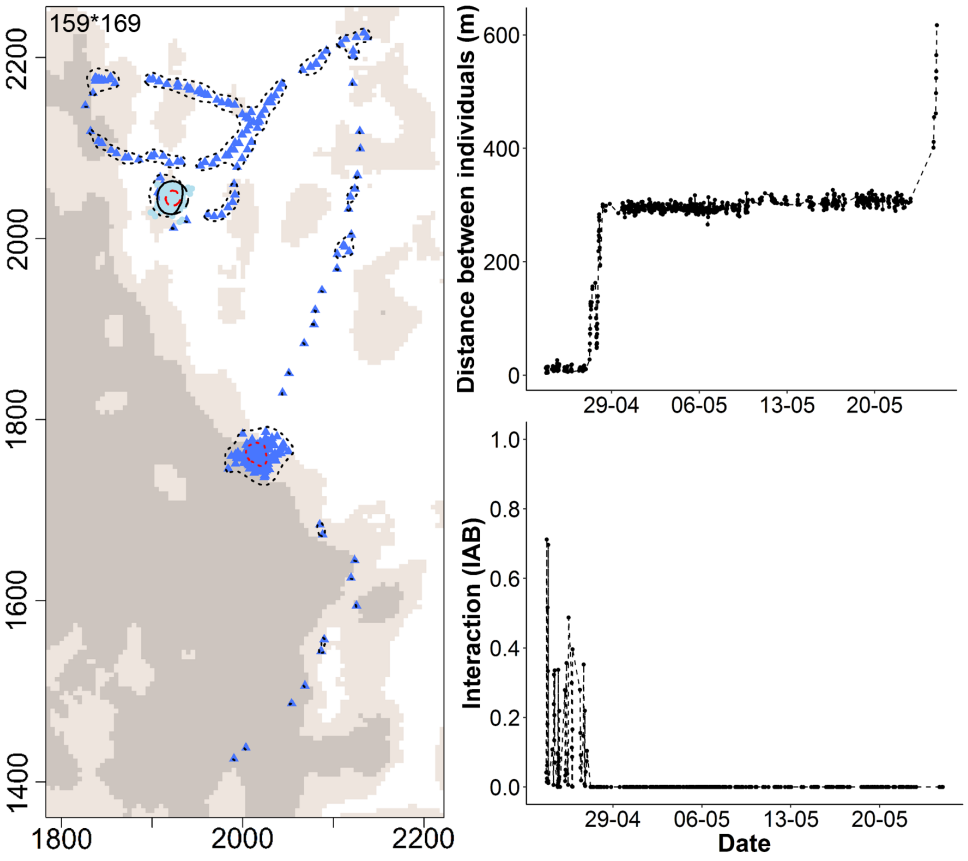

Figure 3.8: Movement and home-range overlap of mixed sex dyad 159α 169β. a) dark blue points and dashed line = α, light blue points and dotted line = β, red line = 50UD and black line = 95UD, b) distance between dyad, and c) interaction index over time.

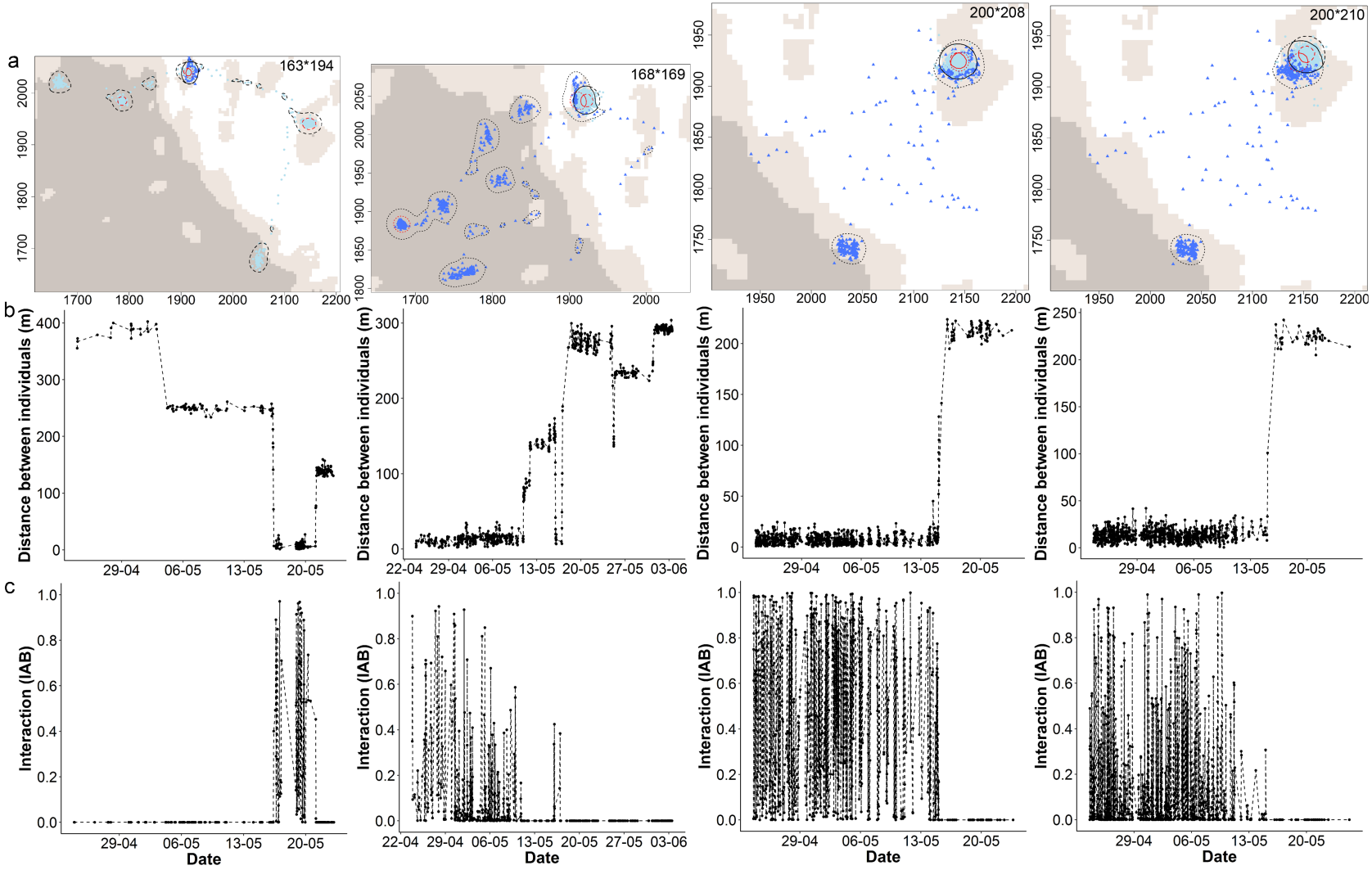

Figure 3.9: Movement and home-range overlap of mixed sex dyads $\alpha\beta$ where one individual has more than one centre of activity during tracking. a) dark blue points and dashed line = α, light blue points and dotted line = β, red line = 50UD and black line = 95UD, b) distance between dyad, and c) interaction index over time.

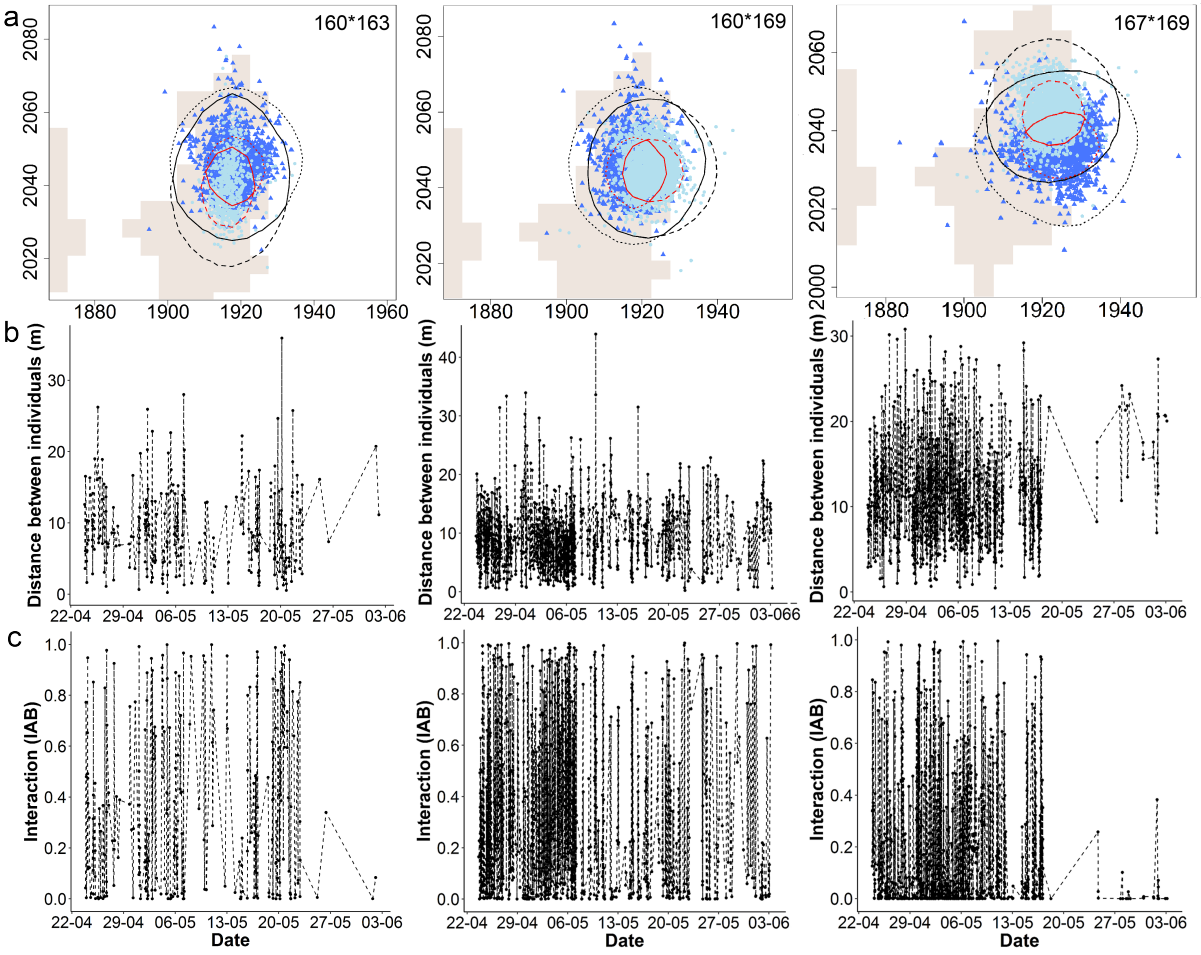

Figure 3.10: Movement and home-range overlap of mixed sex dyads $\alpha\beta$ that exhibited limited movement during tracking. a) dark blue points and dashed line = α, light blue points and dotted line = β, red line = 50UD and black line = 95UD, b) distance between dyad, and c) interaction index over time.

3.4 Discussion

This is the first attempt to quantify interaction between free-ranging *H. gammarus*. The sample size was large $n = 34$, and the range of CL representative of the local catchable population (Skerritt, 2014); however, the number of legal size lobsters (CL $\geq$ 87 mm) was small ($n = 4$). There were clear areas of spatial overlap between same and mixed sex dyads, particularly at the edges of hard and mixed substrate, underlining the importance of shelter providing habitat for lobsters (Cobb, 1971; Howard, 1980; Bowlby et al., 2007). Several lobsters interacted with more than one other, either by having multiple centres of activity, such as lobster 194, or by interacting with multiple individuals that remained within close proximity, such as lobster 160 and lobster 169, highlighting the high degree of individual variation in movement patterns (Skerritt et al., 2015). However, it is important to acknowledge that the number of tagged lobsters was a small proportion of the true population and that lobsters were likely interacting with, and responding to, other untagged conspecifics throughout the study.

3.4.1 Space use and home-range overlap

The size of home-ranges were smaller than previous studies (Moland et al., 2011b; Wiig et al., 2013), differences in size are likely due to the longer time scale of previous studies (242-354 days, Moland et al., 2011b) and the different tracking methods used, i.e. mobile-tracking (Moland et al., 2011b), and 30 min centres of activity (Wiig et al., 2013) which can over estimate UD size (Simpfendorfer et al., 2002). Skerritt et al. (2015) previously investigated the size of *H. gammarus* home-ranges using these data and further details can be found therein. The purpose of this study was to investigate the home-range overlap of *H. gammarus* as part of a hierarchical analysis of lobster interactions. There was broad agreement between BA and UDOI at both the 95UD and the 50UD. Although BA was higher in all cases, except where UDOI produced values > 1, the degree of overlap between dyads was ranked similarly. There was a relatively small number of female only dyads (BA > 0.2). The larger number of male and mixed dyads was therefore likely driven by the larger home-ranges of more mobile male lobsters with multiple areas of activity (Skerritt et al., 2015) overlapping with the home-ranges of the more sedentary females. The majority of female-only dyads shared space on hard substrate, but the majority of male only and mixed sex dyads shared space on mixed substrate. This is again reflective of the importance of shelter providing habitat (Cobb, 1971; Howard, 1980; Bowlby et al., 2007), and the larger home-range areas of the more mobile male lobsters (Skerritt et al., 2015).

3.4.2 Proximity and contact rates

Only a small number of dyads that experienced simultaneous detections (559 dyads) were also proximal (45 dyads = d_c10, 33 dyads = d_c5, 16 dyads = d_c1). Contacts were highest between 1800 h and 0600 h reflecting the lobsters increased activity during hours of twilight and darkness (Smith et al., 1999, 1998c,b; Meeren, 1997; Scopel et al., 2006), and subsequent increased rates of detectability. Interactions between lobsters were only quantifiable if both lobsters were outside of their shelters, it is therefore possible contact rates could have been underestimated due to shelter-related behaviour, although consideration was given to the choice of t_c in order to minimise this effect. Lobsters from the full range of sampled CL interacted, apart for the very largest individual (CL 98 mm). The difference in CL between paired individuals was similar regardless of *dc*. This was possibly due to the availability of suitably sized shelters driving the distributions of similarly sized lobsters (Cobb, 1971; Howard, 1980; Bowlby et al., 2007); however, it could also be due to the over representation of some lobsters due to interactions with more than one conspecific. The number of female-only dyads that interacted remained similar at all values of d_c, but the numbers of male-only dyads reduced when d_c = 1, and mixed sex dyads were reduced at d_c = 5 and below. Previous work (Skerritt et al., 2015) has suggested that female *H. gammarus* are more sedentary than males which may explain contact at small values of d_c. A larger number of interactions by large males has been previously linked to mate competition, although not causally (Karnofsky and Price, 1989b). Males in this study were involved in the largest number of dyads at all values of d_c. There were a number dyads with overlap of the 95UD that had a small values of BA and a 0 value for Prox. This is due to the UD estimation including empty space, and highlights the advantages of dynamic approaches when quantifying interaction and space sharing.

3.4.3 Space sharing and interactions

Statistically significant attraction interactions were identified at Δ = 10 m, and both attraction and avoidance was identified when Δ = 7.5 m and Δ = 5 m. This suggests that Δ = 10 m was potentially too large to identify true behavioural interactions between dyads and was likely describing a larger scale relationship between lobsters and their preferred habitat (Cobb, 1971; Howard, 1980; Bowlby et al., 2007); for example they may have been attracted to the habitat, not each other. Both male and mixed sex dyads exhibited limited movement during the tracking period, and although the proximity of lobsters was similar, male dyad interactions were classed as avoidance and mixed sex dyads were classed as attraction. These apparent differences between mixed sex and male dyad interactions are more pronounced when considering that some lobsters were involved in multiple interactions, where male lobsters avoided male lobsters, while being attracted to female lobsters in the same

time period. Although there was only one female dyad several female lobsters were attracted to more than one male. It is not possible from these analyses to determine which lobster instigated the interaction. In the case of avoidance interactions involving lobster 210, avoidance of conspecifics due to a damaged claw could be possible (Karnofsky et al., 1989a), although lobster 160 did not appear to be similarly affected. Male-male avoidance could be suggestive of small scale spatial exclusion of other males. Aquarium experiments have found that male lobsters will occupy a centrally located shelter and exclude other inhabitants, not only of the occupied shelter, but also from surrounding shelters (Karnofsky and Price, 1989b). A previous study has suggested that in field studies there is less aggressive behaviour exhibited by *H. americanus* than that documented in aquarium studies, due to potentially artificially high stocking densities in tanks (Karnofsky and Price, 1989b). The only avoidance interaction between a mixed sex dyad 159α 169β was characterised by the short time period the two lobsters spent close to one another before the male (lobster 159) undertook longer range movements; when this was reanalysed using only data with the intersecting 95UD, the interaction was no longer significant. A similarly short period characterised the attraction between 163α 194β; however, this remained a significant attraction after reanalysis. It is not clear if the non-significant interaction between 159α 169β in the reanalysis was due to the small number of positions, or to the scale at which the data were subsampled.

As the distance at which lobsters are aware of each other in the field is not known, conservatively small values of Δ were used. The observed value of interaction for avoidance is by definition required to be a small number; however, low observed values that have resulted in statistically significant attraction, such as 168α 169β when Δ = 5 m (Table 3.4), suggest that joint movement occurred very infrequently in these dyads (Benhamou et al., 2014). In this case Δ was probably underestimated and joint movement occurred, but at a larger distance. The significance of these interactions is likely to be poorly estimated, and it is important to remember that a statistical difference does not equate to a biological difference (Johnson, 1999). In the case of 168α 169β estimation improved once the area was reduced to only include the points within the respective 95UDs (Table 3.5). This highlights the need to consider the scale of movements when investigating interactions. Although a hierarchical approach was implemented only a small proportion of lobsters interacted. It is possible that the differences in interaction classification between male and mixed sex dyads are an artifact of habitat availability, or a chance spatial organisation of individuals, therefore behavioural interpretation of these results should be done with caution.

IAB was chosen over path-based indices (e.g. DI (Long and Nelson, 2013) and Cr (Shirabe, 2006)) as it takes account of the distance between individuals (Benhamou et al., 2014). Behavioural interactions between lobsters are reliant on olfactory cues and are likely to occur at close proximity; however, at times during tracking lobsters

were in excess of 100 m from a simultaneously detected lobster, if distance had not been considered, spurious interactions without biological context might have been included. Although IAB was assessed with a range of Δ and t, the distance over which an olfactory signal could be detected will likely rely on current speed and direction (McQuinn et al., 1988); these were not measured as part of this study.

Fine-scale behaviours exhibited by lobsters, such as tail-flipping, were unlikely to be captured due to the transmission delay of the tags (5 min). The analyses undertaken were only able to measure proximity and behaviour in terms of broadly positive or negative space-sharing, and were unable to incorporate fine-scale behaviours and differing levels of aggression (Scrivener, 1971). For example, the close contact, approach-retreat behaviours that are important in assessing the status of conspecifics (Karnofsky and Price, 1989b) were unable to be identified or inform results. This highlights some of the limitations of using tracking data to infer behavioural mechanisms and the importance of validating behaviour data. However, using divers to collect behavioural observations of benthic organisms in open water is costly, logistically difficult, and can only be conducted in fair conditions. Previous studies have used mesocosms (Watson III et al., 2009), or shallow coastal sites (Karnofsky et al., 1989a). While providing greater experimental control and reliable working conditions these setups are often not representative of the condition within the wider ecosystem. One possible solution would be the use of an acoustic tag with an integrated accelerometer, e.g. Vemco (AMIRIX Systems Inc., Halifax, Canada) V13AP (Jury et al., 2018). Although accelerometers are becoming increasingly popular in terrestrial and marine tracking studies, their use during field deployments has largely been restricted to teleosts (Stehfest et al., 2015; Pedersen et al., 2008) and elasmobranchs (Leos-Barajas et al., 2017b), (although see, Goldstein et al., 2015; Lyons et al., 2013; Jury et al., 2018). Aquarium experiments have utilised accelerometers to study lobster behaviour (Goldstein et al., 2015; Lyons et al., 2013) and initial mesocosm studies have correlated activity with distance moved (Jury et al., 2018). However, the attachment method and biological interpretation of data require additional validation across life-histories prior to field deployment (Broell et al., 2013; Jury et al., 2018).

3.4.4 Conclusion

There was evidence of both broad and fine-scale space-sharing, and interaction amongst the lobsters in this study. All three analytical approaches were in broad agreement, highlighting the greater mobility of males, resulting in greater space-sharing in terms of home-range overlap, and a larger number of fine-scale interactions with conspecifics. Fishers already use areas where they believe higher densities of target species exist. These results further illustrate the non-random

distribution of lobsters in relation to habitat and provide an understanding of habitat use, space-sharing and behaviour that could not be achieved in tank experiments, underlining the usefulness of acoustic telemetry in understanding the movements of hard to study species in the field. This approach, together with capture-mark-recapture data and habitat level substrate maps, could provide valuable insight into the spatial and temporal variability in the distribution of individuals, as well as information useful to fisheries management and protected area designation.

The human world, it's a mess.
Life under the sea is better than anything they've got up there..

Sebastian

Chapter 4. Investigating movement patterns of European lobsters, and identifying potential drivers of movement and behaviour change

4.1 Introduction

The behaviour of individuals within a population can be highly variable, and related to body size (Shepherd and Clarkson, 2001), food availability and hunger (Walker et al., 1999; Moore and Howarth, 1996), environmental conditions (Tuomainen and Candolin, 2011), and reproduction (Ru et al., 2017). Yet how behaviour varies and changes through time is an often neglected source of bias within stock assessment models that assume all individuals are equally available to the fishery (Stoner, 2004). While there is evidence of non-constant catchability for a number of fished species (see review Wilberg et al., 2010), this assumption is particularly problematic for decapods (Miller, 1990), many of which are commercially important.

Movement rates of *Homarus* spp. correlate with environmental conditions (Smith et al., 2001; Bowlby et al., 2007; Jury and Watson, 2013), time of day (Scopel et al., 2006), and seasonal resource availability (Bowlby et al., 2008). Two potential movement states, 'resident' and 'transient' have been described for *H. americanus* (Ennis, 1984; Bowlby et al., 2007, 2008). Currently there is no evidence of more than two behavioural states in *H. gammarus* (Moland et al., 2011a). Although movement rates of *Homarus* spp. can be highly variable between individuals (Skerritt et al., 2015) the influence of sex, body size, or reproductive state on home range size is unclear. Moland et al. (2011a) and Scopel et al. (2009) found no effect; however, a study by Skerritt et al. (2015) observed that males had a larger home-range than females. Diel and seasonal patterns of activity have been observed for *H. gammarus* (Smith et al., 1998c, 1999), but the scale of movements made by *H. gammarus* is thought to be generally smaller in magnitude (0.5 m - 1 km e.g. Smith et al., 2001; Agnalt et al., 2007; Moland et al., 2011b; Wiig et al., 2013) in comparison to the large movements recorded for *H. americanus* (90 km e.g. Campbell and Stasko, 1986; Cooper and Uzmann, 1971). Movement patterns of *H. gammarus* can differ depending on the substrate hardness suggesting a potential link between lobster behaviour and substrate composition (Skerritt et al., 2015) and increased mobility has been correlated with increased trap exposure (Wiig et al., 2013) and catchability (Bowlby et al., 2007).

Collecting telemetry data from marine organisms is challenging and often suffers from large periods of missing observations, resulting in highly irregularly data sets.

In the case of marine mammals, high degrees of missingness occur because positions are only recorded when an individual surfaces to breathe and the tag is able to connect to GPS or Argos satellites (Morales et al., 2004; Costa et al., 2010). While acoustic telemetry can facilitate continuous tracking via a Vemco Positioning System, or similar, *Homarus* spp. seek shelter to avoid unfavourable environmental conditions (Bowlby et al., 2007, 2008; Howard, 1980; Howard and Nunny, 1983), to reproduce (Debuse et al., 2003), and to avoid predation (Cooper and Uzmann, 1980; Oppenheim and Wahle, 2013), during which time individuals are unlikely to be detected. As a result telemetry data collected from *Homarus* spp. can suffer from missingness in a similar way to that of the more traditionally tracked marine mammals. However, data gaps from *Homarus* spp., or any other shelter-seeking species, can be considered a fundamental element of their movement process, and indicative of behaviour change. Unfortunately, large errors and large amounts of missingness can restrict the availability of suitable analytical approaches (Gurarie et al., 2009). Behavioural change point analysis (BCPA) (Gurarie et al., 2009, 2016) is a method with few assumptions that identifies changes in behaviour in highly variable and gappy movement data. Change points within a time series are identified by a sweeping window and selected using Bayesian information criterion (BIC) (Gurarie et al., 2009, 2016). Movement metrics (step length and turning angle) are used to derive measures of directionality and velocity of movement; changes in any of the three parameters, mean μ, variance σ, and continuous autocorrelation ρ, or time-scale of autocorrelation τ, can then be identified as an indicator of behavioural change (Gurarie et al., 2009, 2016). BCPA has been used to identify behavioural change points in a variety of taxa, for example, penguins (Zhang et al., 2015), turtles (Mingozzi et al., 2016), tapir (González et al., 2017), as well as acoustically tracked lamprey (Gurarie et al., 2016).

Although BCPA is useful in visualising possible changes in behaviour it does not include covariates that may be considered drivers of behavioural change, and so biological interpretation is limited. Another approach is to assume that the unobserved behaviours present within the movement data belong to different statistical distributions or behavioural 'states' that are characterised by differences in step length and the directionality of movement (e.g 'encamped' vs 'transiting' behaviours, Morales et al., 2004). These state space models are implemented within a Bayesian framework and remain statistically challenging and computationally intensive (Jonsen et al., 2005, 2013, although see Auger-Méthé et al. 2017) as the true behavioural state is often not observed, and depending on the method used (e.g. GPS versus Argos), the positional error of locations can be substantial (Morales et al., 2004; Costa et al., 2010). Hidden Markov models (HMMs) are a special case of state-space model where there are a finite number of latent states (Zucchini et al., 2016) and provide a computationally tractable and mathematically simplistic alternative where

the assumption of negligible error holds true (Langrock et al., 2012; Patterson et al., 2008). They have been used in a wide-range of scientific fields: speech recognition (Bahl et al., 1983), economics (Rydén et al., 1998) and environmental research (Hughes et al., 1999). More recently they have become popular for modelling animal movement (Langrock et al., 2012). Recent software advances that include additional pre-processing, non-stationarity, and multiple imputation (Michelot et al., 2017; McClintock and Michelot, 2017) have widened the applicability of the technique by relaxing the assumption of negligible error and regular time steps; many of the realities of animal tracking, particularly within marine-based studies that include extreme amounts of missing data, irregular sampling, and possibly large measurement error can now be addressed within a HMM framework.

The aim of this study was to investigate the suitability of emerging movement modelling approaches to decipher the potential behaviour states of lobsters using acoustic telemetry data. Due to the behaviour of lobsters, and their habitat preferences, lobster telemetry data is characterised by large and irregular data gaps. Analysis methods specific to missing data (BCPA), or that interpolate missing data points in a realistic manner (multiple imputation HMMs) may be able to offer new insight into the fine-scale movement patterns of lobsters. The effects of environmental covariates on sheltering behaviour were investigated using generalized estimated equations (GEEs), and changes in the behaviour were assessed using BCPA. HMMs were used to identify behavioural states and investigate potential environmental drivers of behavioural change. It was hypothesised that lobster activity would be driven by environmental periodicity in relation to the tide (12.42 h and 12 h periodicity) and time of day (24 h periodicity), and that longer range movements would be associated with areas of varied substrate hardness.

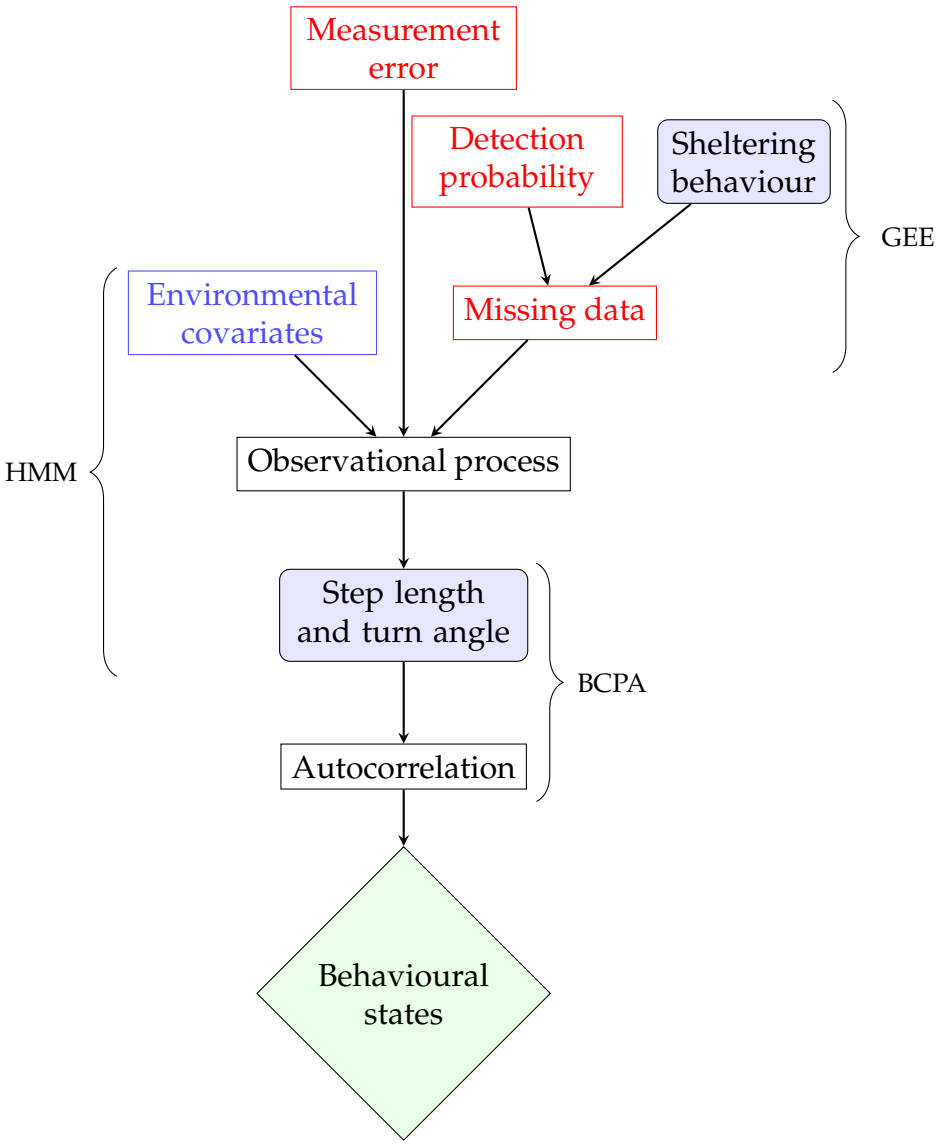

Figure 4.1: Conceptual model of lobster movement. Blue solid rectangles = behaviour, red text = sources of uncertainty, blue text = external drivers of behaviour. Brackets indicate areas of the movement process modelled by each of the analytical approaches.

4.2 Methods

4.2.1 Study site and data collection

Data were collected using a Vemco Positioning System (AMIRIX Systems Inc., Halifax, Canada) deployed approximately 2 km off Blyth, Northumberland UK (approx. 55°07′46″N, 1°26′89″W) between the 23rd April and 3rd June 2013 (Skerritt et al., 2015). Lobsters (n= 44, CL 65-98 mm, Skerritt et al., 2015) were tagged with V13 transmitters (minimum transmission delay of 300 s) and released in the study area within 10 min. Prior to analysis detections with high positional error were identified using linear regression between two measures of horizontal positioning error (HPE and HPEm) (Skerritt et al., 2015; Coates et al., 2013). The model was weighted by the number of HPEm observations per whole value of HPE (see Section 2.2.3). This was to account for the exponential decline in the number of observations as the value of the HPE increased. Observations with a HPE greater than 24 were removed, limiting the maximum error to approximately 10 m and the mean error to approximately 4 m. The first 48 h of tagging data were also removed prior to conducting the analyses to avoid including behaviour resulting from the tagging procedure.

The substrate within the study site was characterised using an Olex AS (www.olex.no) echosounder. Olex software provides a measure of relative hardness on a linear scale between 1 and 100, where 100 is no energy lost; higher values are therefore associated with more reflective materials such rock. Data were subsequently classified as, 'Soft' such as mud and sand < 20, 'Mixed' such as mud and rock > 20 and < 35, and 'Hard' such as continuous rock > 35. It is not possible to infer habitat type using this method as substrate roughness is not measured (Elvenes et al., 2013), however these data are a broad indicator of substrate type and have been previously validated using drop-down cameras in the vicinity of the study site (Skerritt et al., 2015).

4.2.2 Autocorrelation and missing data

Autocorrelation within the data was investigated by first interpolating the missing data points within the lobster tracking data. Missing values were replaced at 5 min intervals, the average transmission delay of the tags, using the next available detected position. Data were then subsampled at different sampling frequencies 5 min, 15 min, 30 min, 45 min, 60 min and 120 min, and the autocorrelation function (*acf* function in R (R Core Team, 2017)) assessed for each subsampled data set.

To identify possible sheltering behaviour logistic GEEs were used to investigate the effect of environmental covariates on the pattern of missing data. Cosine and sine functions of time with varying periods were included as predictor variables to represent cyclical environmental covariates (Stolwijk et al., 1999) day period = 24 h,

day period = 12 h, and tidal period = 12.42 h. Missing observations were replaced as NAs at 5 min intervals to reflect the average sampling frequency of the V13 tags, subsequent NAs were coded as '1' and real observed data points were coded as '0'. The addition of missing data resulted in a lobster data set n = 336063, in order to make the analysis more tractable data were subsampled and only every 30th observation was used, n = 11203, this resulted in a position every 2.5 h. The analysis was repeated using receiver tags with NAs inputted at 10 min (average sampling frequency of receiver tags) and subsampled to every 15th observation n = 4722, to check that any significant effects were not merely artifacts of the Vemco hydrophones detection probabilities under different environmental conditions. Subsampling every 15th observation for receiver tags produced data at the same resolution as the lobster tags, i.e. every 2.5 h. Day 0 and day 41 were removed so only full days of data collection were used. Models had an auto-regressive correlation structure to account for autocorrelation, observations were time ordered, and grouped by lobster ID to account for individual-level non-independence; all models were built using R library geepack (Højsgaard et al., 2006). Lobsters that had more than 100 data points and that were tracked for more than one month were considered in the analysis.

4.2.3 Behavioural Change Point Analysis

BCPA identifies changes in behaviour within an animals trajectory by using a moving window of n animal locations (window size). Behavioural change is the result of a significant change in one or more of three parameters relating to the direction or speed of the animal, i.e. the mean $= \mu$, standard deviation $= \sigma$, and time-scale of autocorrelation $= \tau$. Significant changes in these parameters are defined as 8 separate models (Table 4.1). τ is a continuous measure of the temporal correlation in the movement (Gurarie et al., 2009).

Two measures of behaviour were analysed using BCPA, the persistent velocity (Vp) and log(velocity) ($log(V)$). Analysing movement using Vp identifies changes in the tortuously of movement by including speed and turn angle $(Vp) = Vcos(\theta)$, where V is speed = displacement/time interval and θ is turning angle (Gurarie et al., 2016). Analysing behaviour using $\log(V)$ only considers changes in speed. The chosen window size should correspond to the time scale at which the behaviour is likely to occur (Gurarie et al., 2016; González et al., 2017; Walden-Schreiner et al., 2018). Vp models used window size (w) = 50 and $log(V)$ models used w = 75, both used step size = 1 (data points moved between windows). As the minimum sampling period was 5 min so w = 50 and w = 75 would represent a period of at least 4-6 h during which emergence from shelters, and therefore a change from not moving to moving, would occur. BCPA model selection uses a modified version of BIC

$$BIC = -K\log(L) + k\log(n) \tag{4.1}$$

where L is the likelihood, k is the number of parameters and n is the number of data points, but where a constant $K > 0$ replaces the standard 2, therefore smaller values K result in more conservative model selection (Gurarie et al., 2009). Different values of K were selected to model Vp and $log(V)$, but were kept constant between lobsters in order to make results comparable. BCPA output can be either 'smooth' or 'flat'. Smooth BCPA returns parameter estimates from each data point averaged over all the windows, and flat BCPA returns estimates that are calculated between each of the returned change points (Gurarie et al., 2009, 2016). As such, flat BCPA assumes that behaviour does not vary between change points (Gurarie et al., 2016). The 'threshold' and 'cluster width' of change points for the smooth and flat analyses, refer to the number of times a change point has to be identified before it is reported, and the number of change points to cluster before estimating the parameters between them, respectively (Gurarie et al., 2009). Threshold and cluster width were also kept constant between lobsters to keep tracks comparable, and were chosen to avoid overly complicated models while retaining the ability to discriminate between clear changes in parameters; Vp models used threshold = 12, cluster width = 15, and $K = 4$ and $log(V)$ models used threshold = 6, cluster width = 6, and $K = 1.5$. Lobster tracks were assessed visually and only individuals that had a centre, or centres of activity, and longer range movements beyond these areas were analysed. To further ensure that analysed tracks were comparable, a larger sample size threshold of a 1000 positions that had been tracked for over a month were used in the BCPA analysis.

Table 4.1: Definition of change point models (Gurarie et al., 2009).

Model	Parameters changed
M0	Null model
M1	μ only
M2	σ only
M3	τ only
M4	μ and σ
M5	μ and τ
M6	σ and τ
M7	μ, σ, and τ

4.2.4 Hidden Markov models

Lobster tracks used in the BCPA analyses were subsequently reanalysed using HMMs to investigate the effect of covariates on the probability of transitioning from restricted behaviour to more directional longer range movement. HMMs were built using the R package *momentuHMM* (McClintock and Michelot, 2017). Individual

movement was modelled separately and only lobsters that had been tracked for a month or more, and had 1000 data points were used in the analysis. As raw data were irregular, missing values were first modelled using a continuous-time correlated random walk (CRAWL model (Johnson et al., 2008)); the CRAWL model adjusts for the size of the error and therefore raw data had an HPE ≤ 100. The basic continuous-time correlated random walk model assumes constant motion (Johnson et al., 2008). Due to the shelter-seeking behaviour of *H. gammarus* they cannot be considered to be in constant motion. Sheltering behaviour was modelled by including an activity variable that slows the velocity of the model to zero (Johnson et al., 2008); lobster activity was coded as 0 or 1 depending on whether the detection interval was greater or lesser than a specified time period. For example, if the animal was undetected for more than 2 h then the activity was recorded as 1 and less than 2 h was 0. Two alternative activity variables were modelled, using 1.5 h and 2 h gaps to determine if the lobster was moving; these values correspond to approximately the 90 % and 95 % quantiles and were similar for all lobsters (Fig. 4.2). Due to the slow movement of *H. gammarus*, locations were predicted at 1 h, 2 h and 3 h intervals, which retained the majority of the paths' original characteristics, but reduced the large number of 0 step lengths. The cosine and sine functions used in Section 4.2.2 were used as covariates; the *momentuHMM* package (McClintock and Michelot, 2017) requires that wave periods are whole numbers, therefore 12.4 h was converted to 744 min prior to analyses. Habitat covariates included substrate hardness and depth, and were available from Olex data. Additional habitat information on the variability of the substrate hardness and depth, as well as the distance from an edge, defined as a change in hardness values greater than 30%, were derived from the Olex data (see Section 2.2.2) using ArcMap. Step length was modelled using the gamma distribution with a zero inflation parameter, and turn angle was modelled using the wrapped Cauchy distribution. The wrapped Cauchy distribution is a standard distribution with fat tails used to model animal movement turn angles (Morales et al., 2004; Yackulic et al., 2011). There are two parameters: the mean μ and the mean cosine of the angular distribution p which is bounded by 0 and 1, where 0 is a uniform distribution and 1 is a concentrated distribution around μ. In an attempt to maximise the global likelihood function initial parameters were randomly replaced 50 times (Michelot et al., 2016b; Langrock et al., 2012).

Hidden Markov model selection can be difficult, with a tendency for more complicated models to be selected regardless of biological relevance, as such, a pragmatic approach to model selection is required (Pohle et al., 2017). Only two states were investigated in this study, state 1 = sheltering/restricted movement, and state 2 = longer range directional movement. Model selection used a 4 step process and all best fit models were selected using AIC, and by examining the pseudo-residuals and the remaining autocorrelation: 1) models containing cyclical covariates and

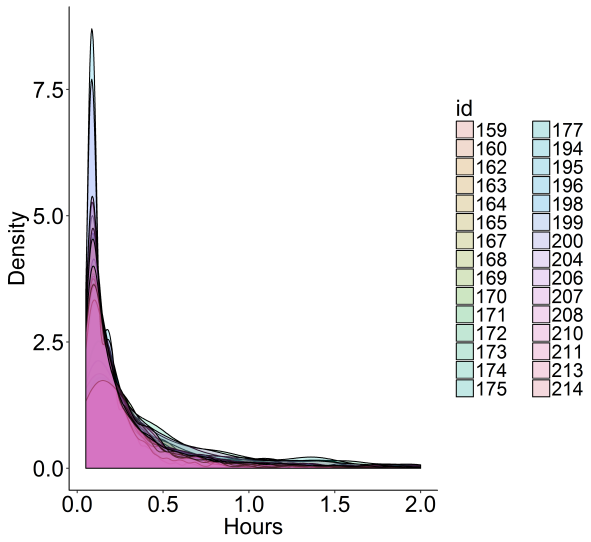

Figure 4.2: The 95 % quantile for the detection period between sequential observations for lobsters that were tracked for more than a month.

environmental covariates were compared separately, i.e. one covariate per model; 2) if models containing a cyclical or environmental covariate were both better than the null model, a more complicated model containing both the top cyclical covariate and the top environmental covariate was fitted. Likewise if more than one cyclical covariate was better than the null model a more complicated model containing both was used to investigate an additive relationship; 3) using the preferred model covariates as identified in steps 1 and 2 a further model was used to investigate if the state distribution parameters were a function of those covariates; 4) finally, the best fit model was then used to simulate n = 100 tracks, model estimates were pooled, and standard errors and confidence intervals were derived to account for the positional error associated with the interpolated data (Equations A.1 and A.2) (Rubin and Schenker, 1986). As environmental covariates were derived from the same Olex data, only one environmental covariate was included in a model due to the possibility of collinearity.

4.3 Results

4.3.1 Autocorrelation and missing data

There were 30 lobsters that had at least 100 detections and had been tracked for at least a month. The autocorrelation functions for lobster step length indicate non-stationarity; cyclical patterns within lobster step length became more apparent as the sampling period increased (Fig. 4.3 and Fig. 4.4).

Neither the 12 h or 12.42 h periods that represented the tidal cycle were significant predictors of periodically missed lobster detections (sine 12 h p = 0.41, cosine 12 h p = 0.24, and sine 12.42 h $p < 0.001$, cosine 12.42 h p = 0.14). A simplified model

containing only 24 h periodicity was fitted; there was a significant effect of the time of day on the periodic probability of missed lobster detections (sine 24 h $p = 0.002$, cosine $p < 0.001$). There were no significant cyclical predictors of periodically missing receiver tags detections (Table 4.2).

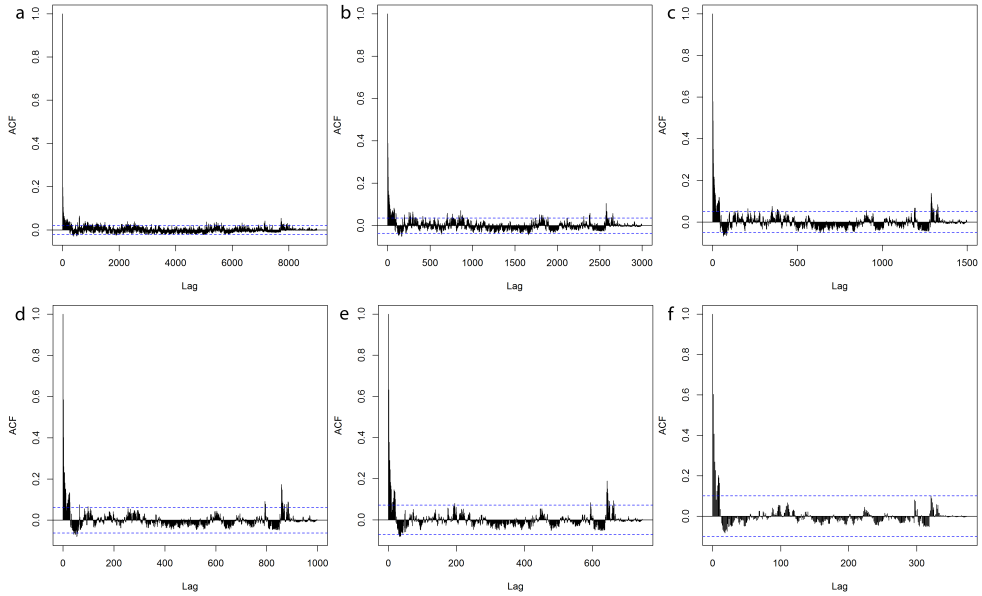

Figure 4.3: The autocorrelation function of lobster 159 at increasing time intervals. a) 5 min, b) 15 min, c) 30 min, d) 45 min, e) 60 min, f) 120 min. Lag is one unit of the sampling period.

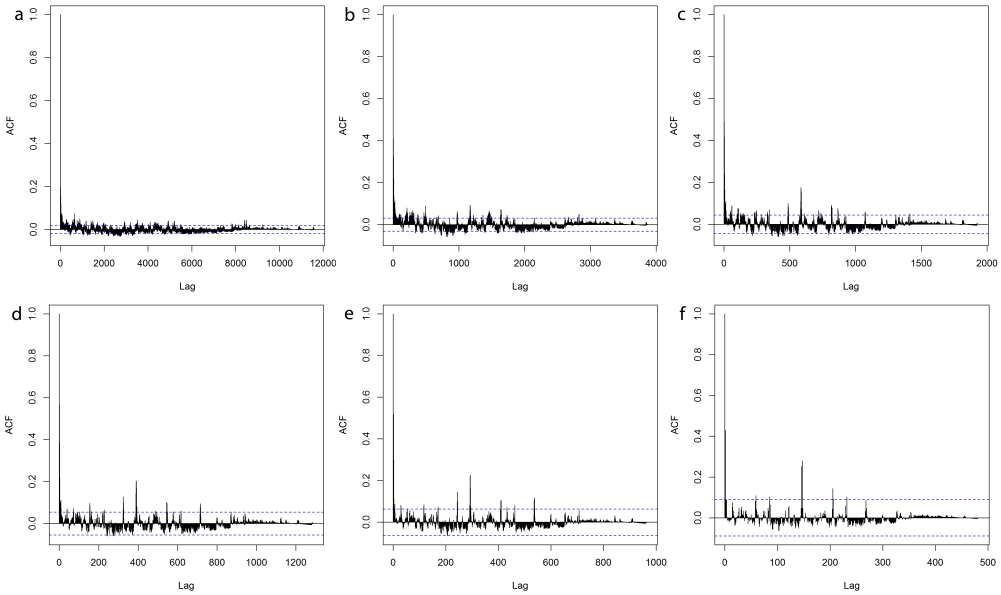

Figure 4.4: The autocorrelation function of lobster 194 at increasing time intervals. a) 5 min, b) 15 min, c) 30 min, d) 45 min, e) 60 min, f) 120 min. Lag is one unit of the sampling period.

Table 4.2: Effect of environmental periodicity on missing receiver positions.

Parameters	Estimate	s.e	Wald	p
Intercept	-4.99	7.92	0.40	0.53
sine 12.4 h period	-23.06	51.06	0.20	0.65
cos 12.4 h period	-31.42	31.67	0.98	0.32
sine 12 h period	34.03	42.67	0.64	0.43
cos 12 h period	-2.45	30.42	0.01	0.94
sine 24 h period	-6.43	13.57	0.22	0.64
cos 24 h period	-6.55	7.77	0.71	0.04

4.3.2 Behavioural Change Point Analysis

There were 20 lobsters that had more than 1000 positions and had been tracked for one month or more, but there were only 8 that appeared to exhibit directional movement (Fig. 4.5). Selecting an appropriate value of constant K that could be used consistently across individuals was challenging. A smaller number of behavioural change points were selected for the Vp analyses compared to the $log(V)$ analyses (5 to 10 and 10 to 25, respectively). The parameter σ changed most often in Vp flat analysis (M2 Table 4.1). When there was a change in more than one parameter the most frequent combination was a change in μ and σ (M4 Table 4.1). There was only a change in more than 2 parameters for 2 lobsters, lobsters 159, and 168 (M7 a change in μ, σ, and τ, Table 4.1). A change in μ only was the most frequently selected model for $log(V)$ flat analysis (M1 Table 4.1); lobster 214 was the only lobster to change in all 3 parameters. The vast majority of mid-points between identified behavioural changes were between 1900 h and 0600 h. For brevity only two lobsters are discussed in detail here and additional lobsters are presented in Appendices: A.1.

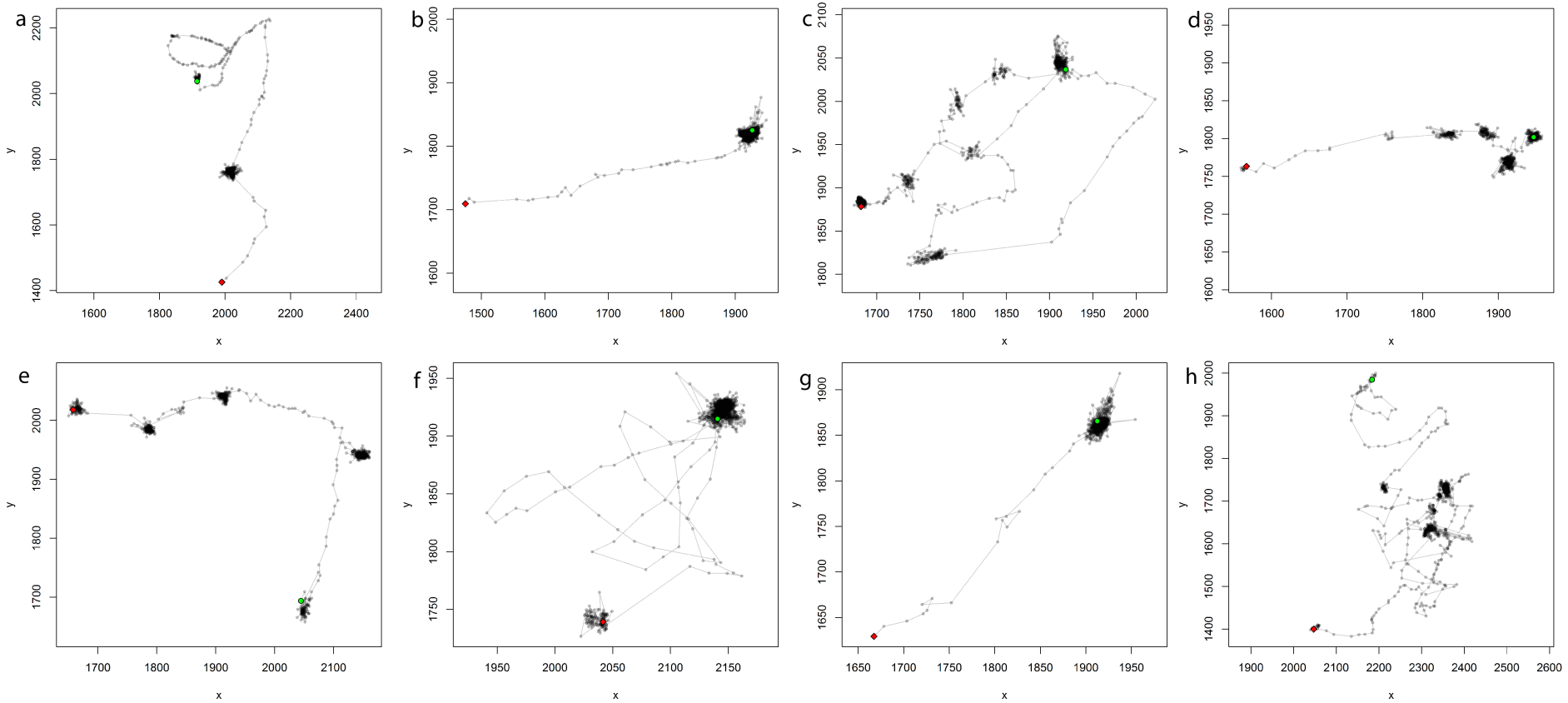

Figure 4.5: Lobsters that were tracked for more than a month, had 1000 detections or more, and exhibited directional movement. a) lobster 159, b) lobster 165, c) lobster 168, d) lobster 170, e) lobster 194, f) lobster 200, g) lobster 204, h) lobster 214. Green dot = track start point, and red square = track end point.

The more directional movement by lobster 168 was identified by both the smooth and the flat analyses (Fig. 4.6). BCPA analyses identified restricted or encamped behaviours as those with negative μ values, and directional behaviours had larger τ values and larger μ and σ values (Fig. 4.6c and Fig. 4.6f). The smooth BCPA analyses for lobster 200 (Fig. 4.7) and lobster 160 were similar, in both cases directional movement was associated with larger values of τ and an increase in μ and σ (Fig. 4.7a - Fig. 4.7c). The flat BCPA differentiated all of the directional movement (large τ) from the restricted tortuous movement (lobster 200, Fig. 4.7d - Fig. 4.7e), and there was a smaller range of σ values associated with the restricted movement compared to lobster 168 (Fig. 4.6f and Fig. 4.7f, respectively).

The $log(V)$ analyses produced more variable results compared to the Vp analyses. Smooth BCPA did associate larger τ values with larger values of $log(V)$ (lobster 168, Fig. 4.8a - Fig. 4.8c), but the flat BCPA did not produce such a clear distinction between fast and slow movement (Fig. 4.8d - Fig. 4.8e). The $log(V)$ analysis for lobster 200 was also variable and potentially misclassified behaviour during the smooth and flat BCPA, (Fig. 4.9a - Fig. 4.9e). In both smooth and flat BCPA the σ is relatively constant for the lower values of τ; however, large values of τ were associated with the full range of μ values in the smooth analysis (Fig. 4.9c). Likewise there was no differentiation between small and large values of μ in the flat analysis (Fig. 4.9f). Although flat analyses and smooth analyses are not directly comparable due to the differing definitions of 'threshold' and 'cluster width' flat analyses using Vp and $log(V)$ consistently selected more change points during times of restricted movement than were identified by the smooth analyses, (Fig. 4.6 - Fig. 4.9). Overall the models using $log(V)$ were a better fit and did not suffer from the extreme values associated with the Vp analyses (Fig. 4.10).

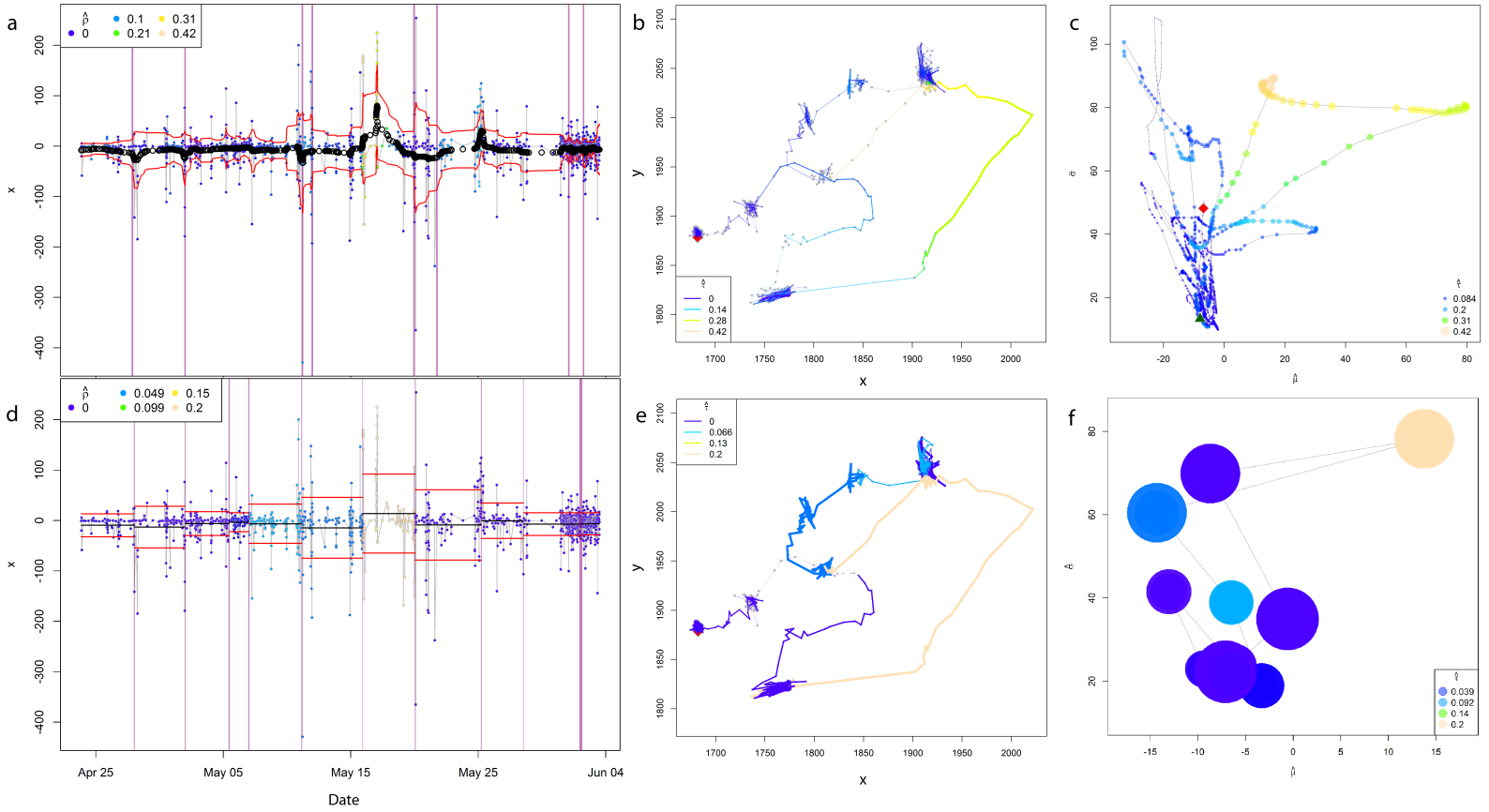

Figure 4.6: BCPA analysis using the persistence velocity (Vp) of lobster 168, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 168 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 168 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

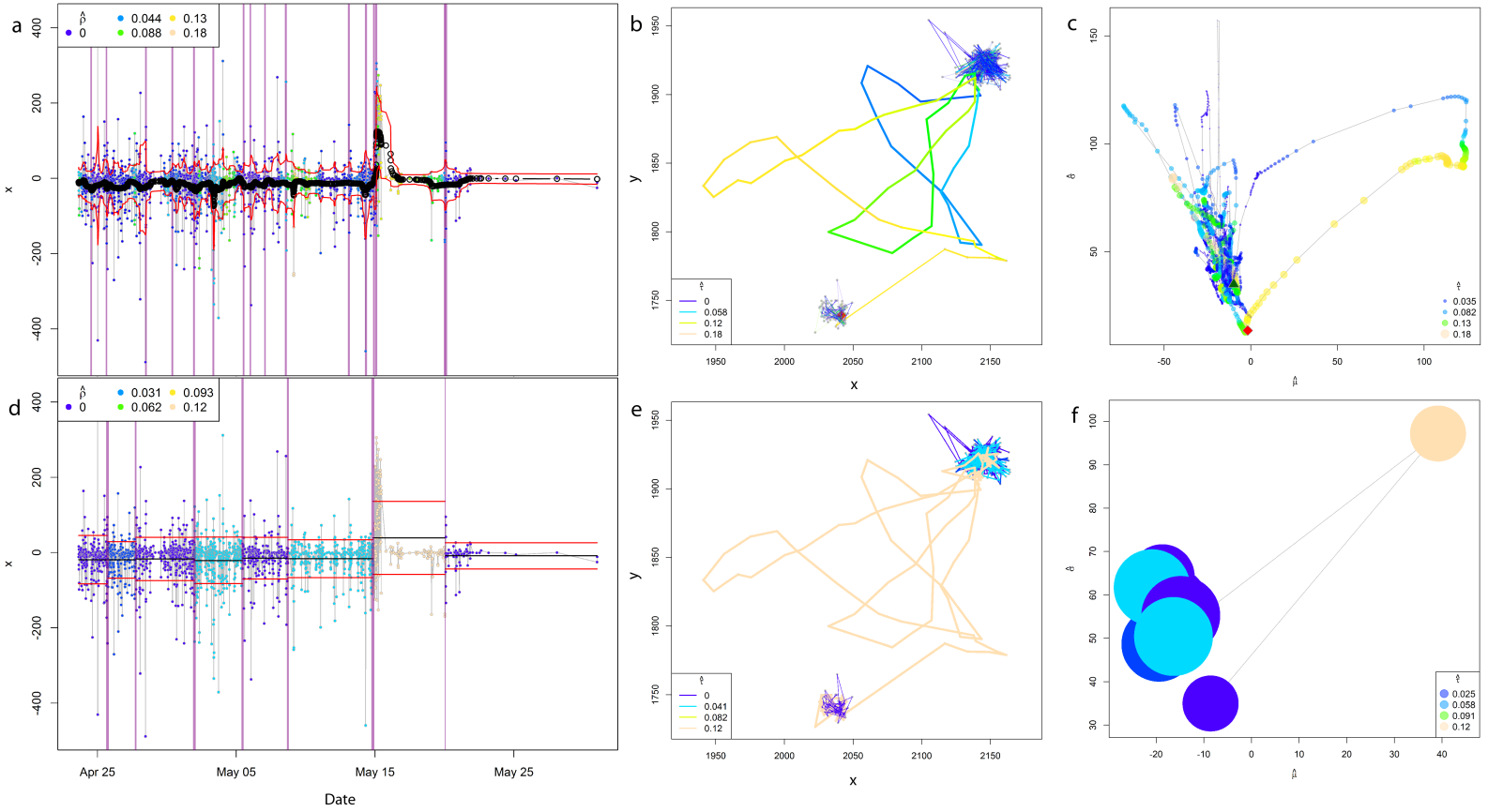

Figure 4.7: BCPA analysis using the persistence velocity (Vp) of lobster 200 $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 200 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 200 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

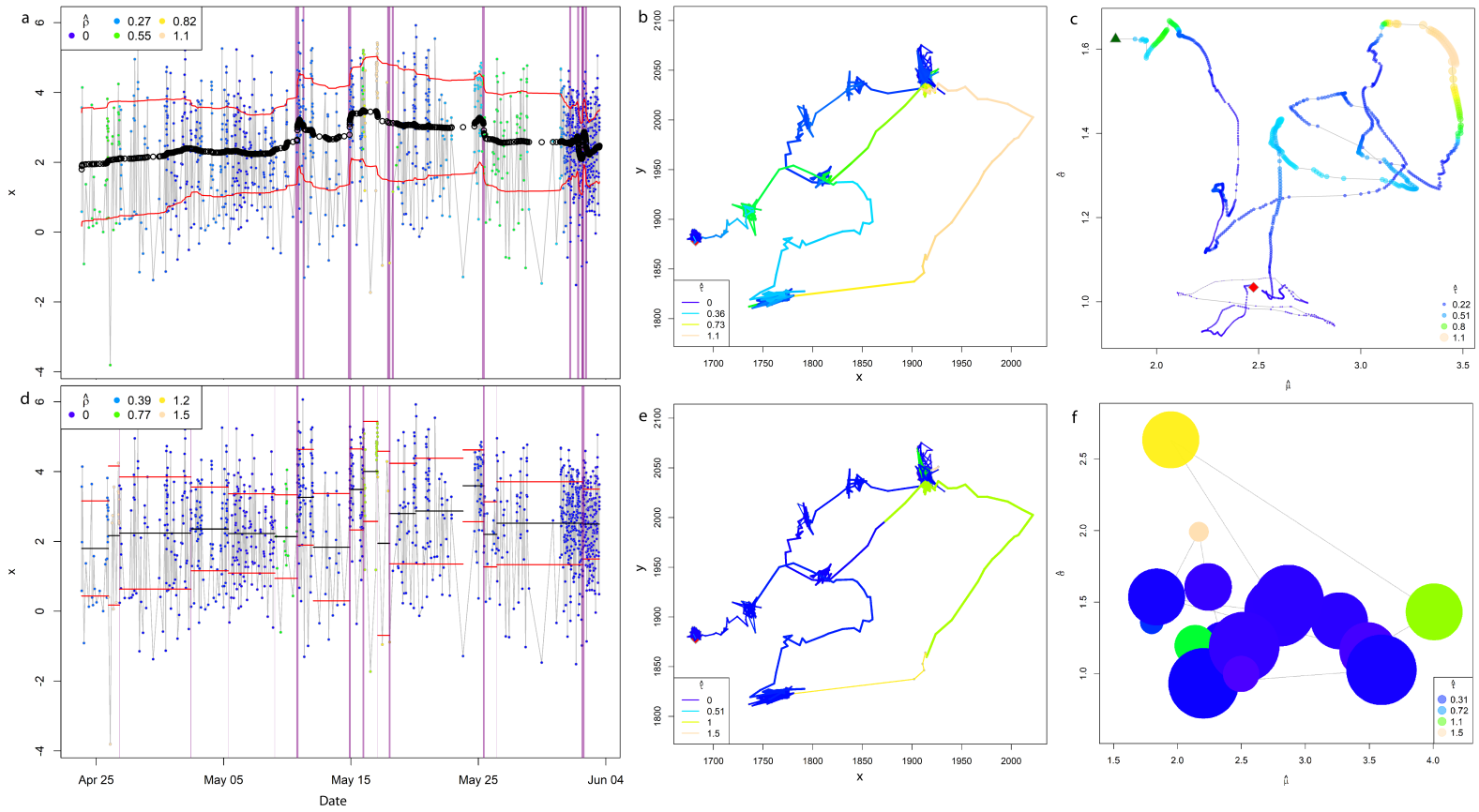

Figure 4.8: BCPA analysis using the log velocity $log(V)$ of lobster 168, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 168 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 168 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

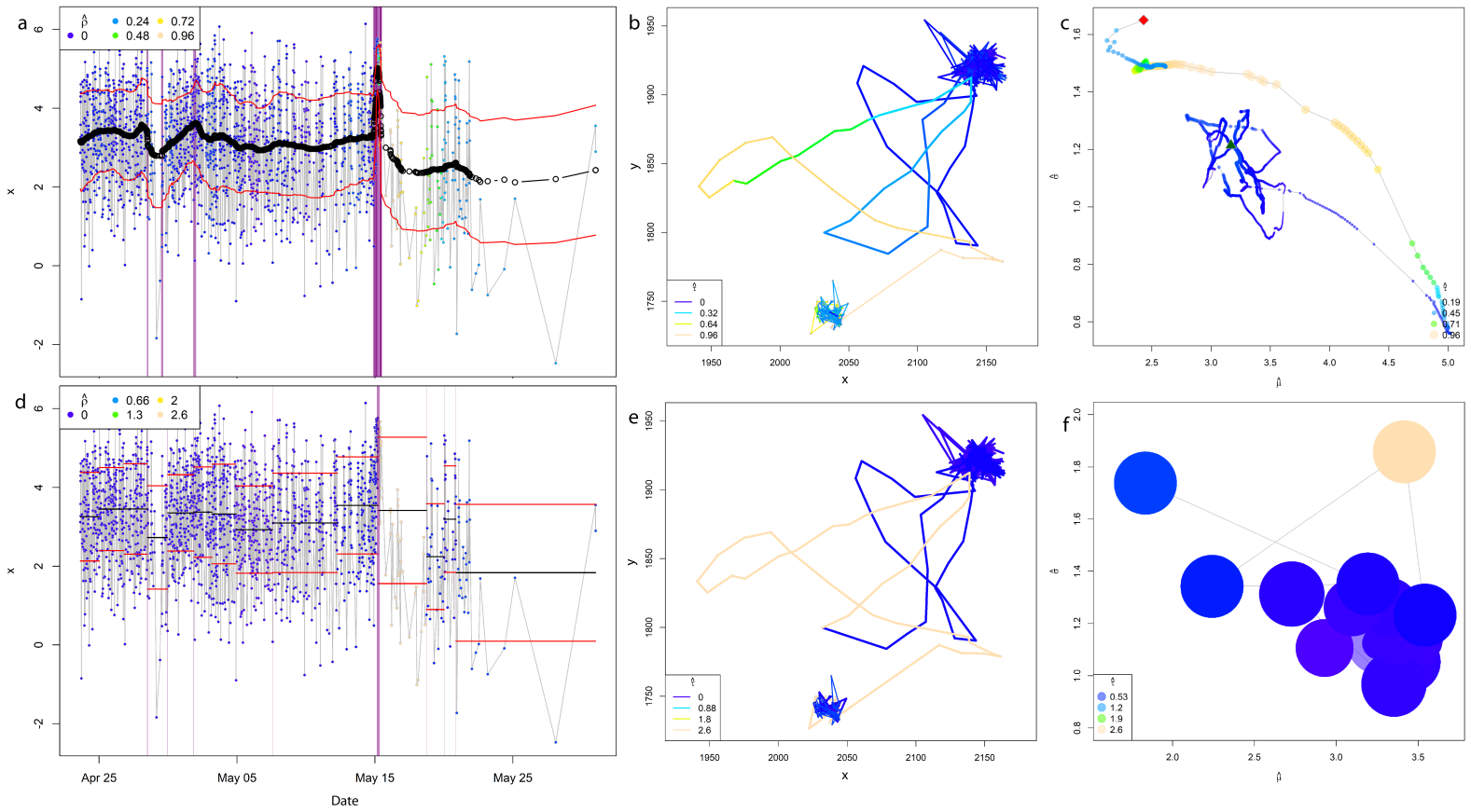

Figure 4.9: BCPA analysis using the log velocity $log(V)$ of lobster 200, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 200 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 200 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

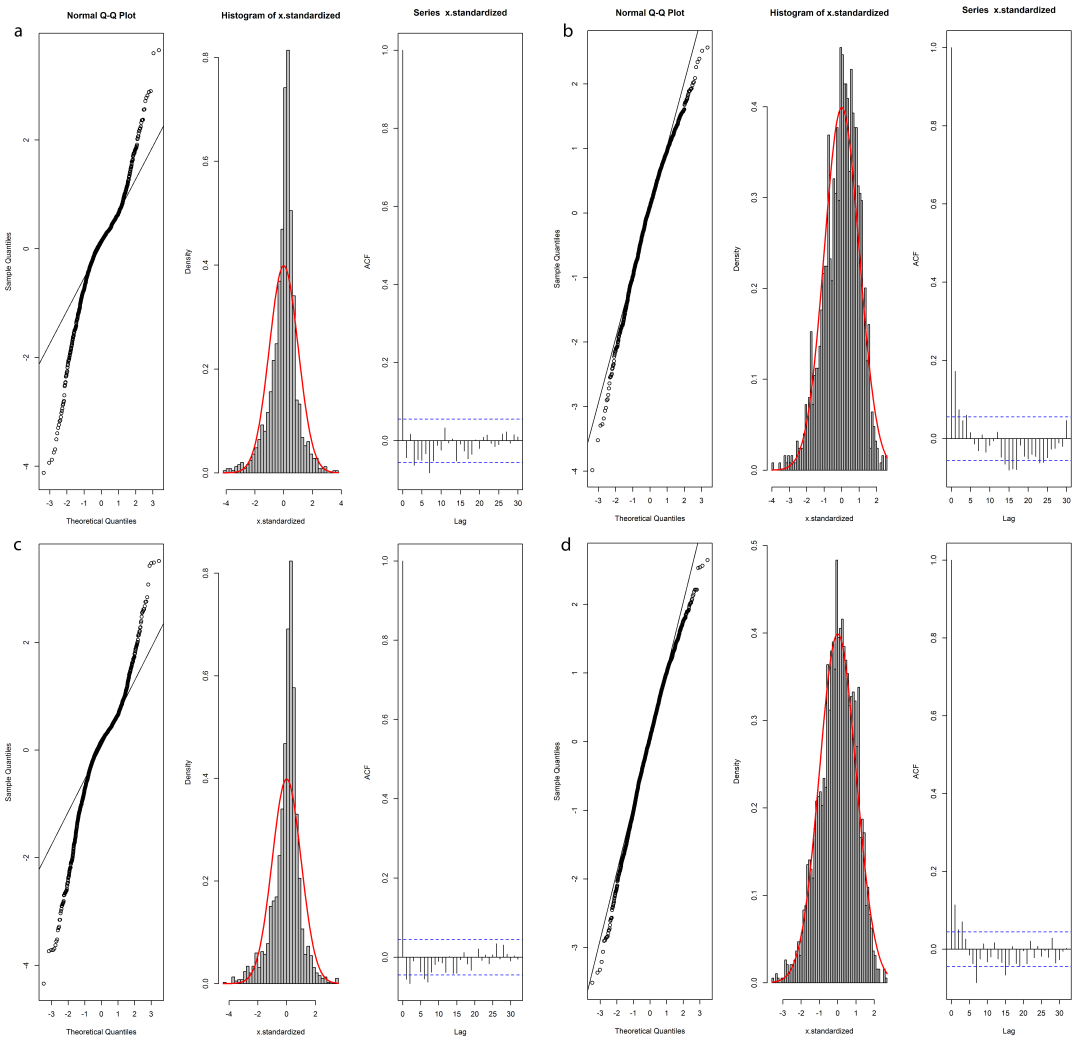

Figure 4.10: Diagnostic plots from BCPA analyses Fig. 4.6-Fig. 4.9. a) persistence velocity of lobster 168, b) log velocity of lobster 168, c) persistence velocity of lobster 200, d) log velocity of lobster 200. Within a-d left = qqplot, middle = histogram of the standardised residuals, right = autocorrelation function of the standardised residuals.

4.3.3 Hidden Markov Models

There was evidence of two behavioural states of the European lobster identified by the HMMs; however, only a small number of models converged using multiple imputation (Table 4.3 and Fig. 4.11 - Fig. 4.14). The drivers of movement differed between individuals, but changes in the probability of transitioning from state 1 (resting/restricted movement) to state 2 (longer movements) were influenced by the tidal cycle (12.4 h cycle, lobsters 159 and 204, Fig. 4.11 and Fig. 4.14, respectively) and the time of day (24 h cycle, lobster 168 Fig. 4.12). Lobsters that were influenced by the tidal cycle had a higher probability of transitioning from state 2 to state 1 in the 2 hours after high tide compared to the later half of the tidal cycle when they were more likely to transition into state 2 and undertake long range movement (Fig. 4.11c and Fig. 4.14c). Lobster 168 had a lower probability of transitioning from state 2 to state 1 between the hours of 0500 and 1000, and subsequently a higher probability of being in

state 2 compared to state 1 during these times (Fig. 4.12a and Fig. 4.12c). There was also evidence of the importance of edge habitat for longer range lobster movement (Fig. 4.13). Lobster 170 had a higher probability of transitioning from state 1 to state 2 with increasing contrast between substrate (Fig. 4.13c) and therefore being in state 2 when there was the greatest contrast between substrate values (Fig. 4.13d); there was equal probability of lobster 170 being in either state in areas where substrate was less variable. Where environmental covariates improved models, such as hardness slope and depth slope, they often performed similarly and with less than 2 AIC between models, underlining the importance of edge habitat, but also the possible collinearity between depth and substrate change. There were some issues with the CRAWL best fit models, and the multiple imputation models. The confidence intervals associated with state 2 were large and in some cases spanned 0 (Table 4.4). There was also a large number of turns centred on π (Fig. 4.11b - Fig. 4.14b), that were not present in the best fit models, and that were not accounted for in the modelled distributions; these turns either belong to a further third movement state, or are an artifact of the multiple imputation, i.e. error associated with small movement steps (Pohle et al., 2017).

Initial CRAWL models were sensitive to the predictive time step used. Models with cyclical covariates, such as, 12.4 h or 24 h periodicity were not selected as the best fit models at larger predictive time steps (lobsters 159 and 194) and models containing environmental covariates (e.g. hardness slope) were no longer better than the null model (Table 4.3 and Appendices). The multiple imputation step was also sensitive to the number of data points and the predictive time step used, with many models failing to converge successfully at 2 h and 3 h predictive time steps (Table 4.3). Initially the best fit model for lobster 204, using a 2 h activity and a 2 h predictive time step, included both a 12 h cycle and a 12.4 h cycle (Table 4.3). This more complicated model did not converge using multiple imputation, but the simpler 2nd choice model did (12.4 h only, Fig. 4.14). Similarly with lobster 214, the best fit model was a 12. 4 h cycle for the transition probabilities and as a function of step length, this model did not converge using multiple imputation, but a simpler model that included only 12.4 h cycle for the transition probabilities did. There were 12 best fit models that included the covariate as a function of one of the state distribution parameters (Table 4.3), none of these converged using multiple imputation.

Table 4.3: Best fit HMMs based on AIC. If a model containing a covariate was not better, only the null model is presented. Δ AIC is the difference between the best fit HMM and the null model. [a] denotes models that failed to converge using multiple imputation. [b] denotes models that are presented in Fig. 4.11 to Fig. 4.14.

Lobster ID	Activity Interval	Predictive Interval	Model	Δ AIC
159	1.5 h	1 h	12.4 h cycle	29.4[b]
159	1.5 h	2 h	12.4 h cycle	21.3
159	1.5 h	3 h	12.4 h cycle	2.7
159	2 h	1 h	12.4 h cycle	26.6
159	2 h	2 h	12.4 h cycle	2.7
159	2 h	3 h	Depth slope *angle* (°)	49.5
165	1.5 h	1 h	12.4 h cycle	19.14[a]
165	1.5 h	2 h	Depth slope (°) *zeromass*	136.16[a]
165	1.5 h	3 h	Depth slope (°) *zeromass*	163.91[a]
165	2 h	1 h	12.4 h cycle	20.18[a]
165	2 h	2 h	12.4 h cycle	21.44[a]
165	2 h	3 h	Depth slope (°)	3.05
168	1.5 h	1 h	24 h cycle	58.1[b]
168	1.5 h	2 h	24 h cycle *angle*	57.1[a]
168	1.5 h	3 h	Null model	0.0[a]
168	2 h	1 h	24 h cycle	125.6
168	2 h	2 h	24 h cycle + hardness slope (%)	15[a]
168	2 h	3 h	Null model	0.0[a]
170	1.5 h	1 h	Hardness slope (%)	27.4[b]
170	1.5 h	2 h	Depth slope (°)	27.8
170	1.5 h	3 h	Depth slope (°)	10[a]
170	2 h	1 h	Hardness slope (%)	19[a]
170	2 h	2 h	Hardness slope (%) *zeromass*	22.2[a]
170	2 h	3 h	Hardness slope (%) *zeromass*	19[a]
194	1.5 h	1 h	Depth slope (°)	19.8[a]
194	1.5 h	2 h	24 h cycle + Depth slope (°)	43.1[a]
194	1.5 h	3 h	Null model	0.0[a]
194	2 h	1 h	24 h cycle + Depth slope (°)	45.4[a]
194	2 h	2 h	24 h cycle + Depth slope (°)	30.5[a]
194	2 h	3 h	Null model	0.0[a]
200	1.5 h	1 h	12.4 h cycle	7.9[a]
200	1.5 h	2 h	Hardness slope (%)	50.2[a]
200	1.5 h	3 h	Depth slope (°) *zeromass*	10.5[a]
200	2 h	1 h	24 h cycle	13[a]
200	2 h	2 h	Depth slope (°)	220.5[a]
200	2 h	3 h	24 h + Depth slope (°)	15.8
204	1.5 h	1 h	Depth slope (°) *zeromass*	179.7[a]
204	1.5 h	2 h	Depth slope (°) *angle*	84.2[a]

Continued on next page

Table 4.3 – *Continued from previous page*

Lobster ID	Activity Interval	Predictive Interval	Model	Δ AIC
204	1.5 h	3 h	12 h cycle	6.3[a]
204	2 h	1 h	12.4 h cycle + 12 h cycle	55.1[a]
204	2 h	2 h	12.4 h cycle + 12 h cycle	26.6[a]
204	2 h	3 h	Hardness slope (%) *zeromass*	59.2[a]
214	1.5 h	1 h	12.4 h cycle *step*	61.01[a]
214	1.5 h	2 h	Hardness slope (%)	12.82
214	1.5 h	3 h	Hardness slope (%) *angle*	10.83[a]
214	2 h	1 h	12.4 h cycle	52.33[a]
214	2 h	2 h	24 h cycle + 12.4 h cycle	126.76[a]
214	2 h	3 h	Depth slope (°)	21.84

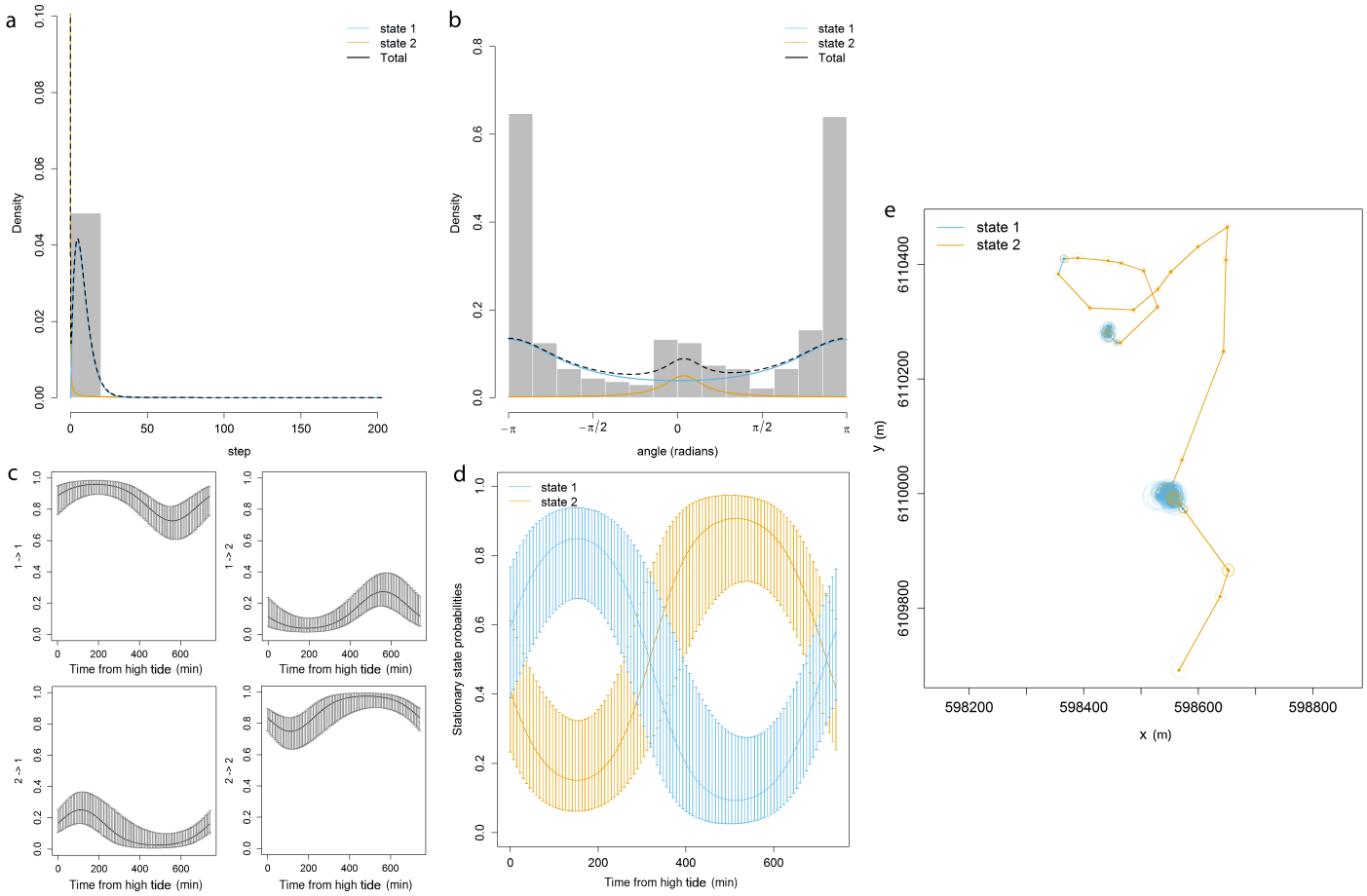

Figure 4.11: Movement process of lobster 159 as a function of time from high tide using multiple imputation. Activity variable = 1.5 h and predictive time step = 1 h. a) step length distribution, b) turning angle distribution, c) transition probabilities, d) stationary state probabilities, e) Viterbi-decoded movement track of lobster 159.

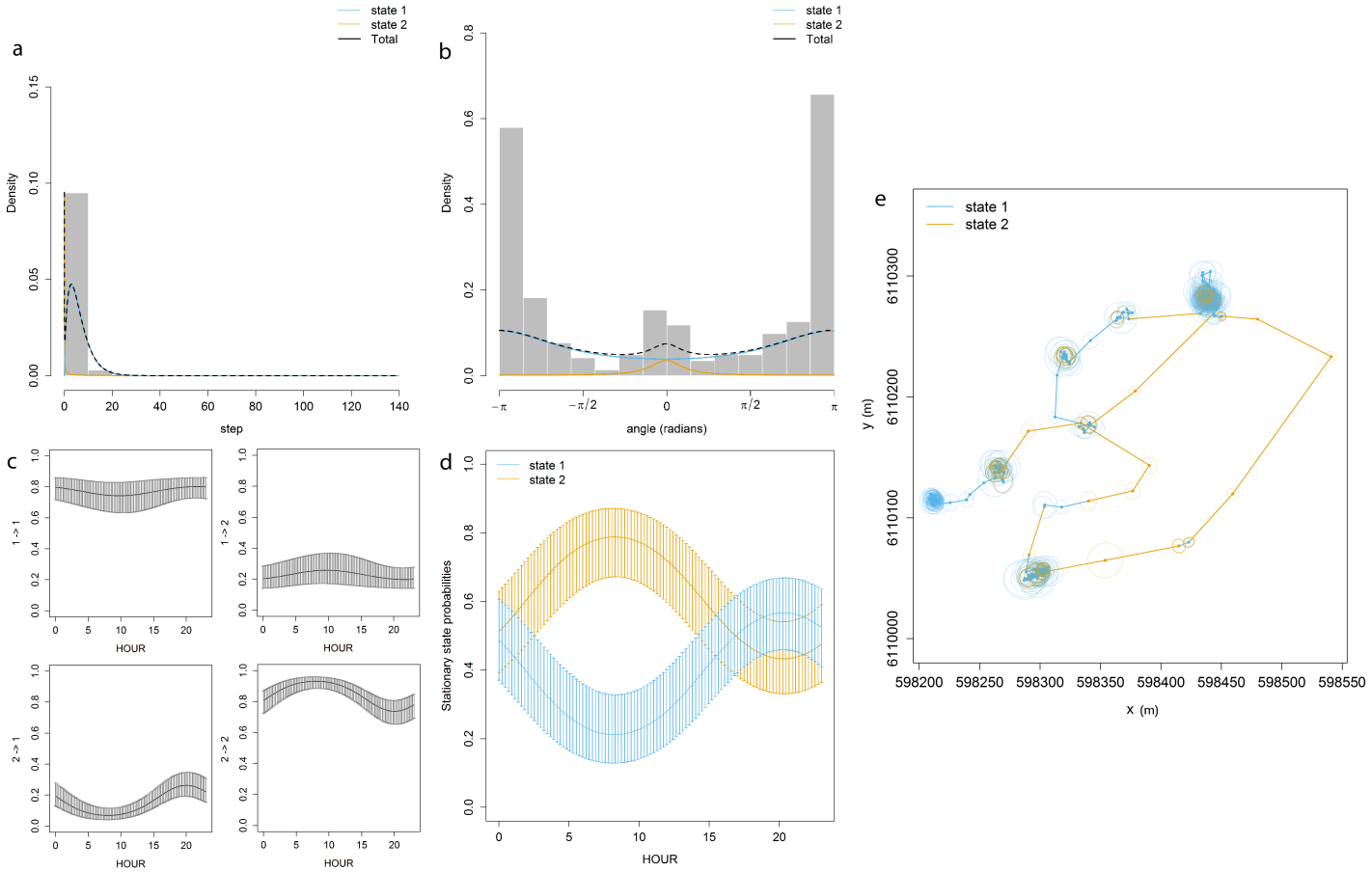

Figure 4.12: Movement process of lobster 168 as a function of time of day (24 h cycle) using multiple imputation. Activity variable = 1.5 h and predictive time step = 1 h. a) step length distribution, b) turning angle distribution, c) transition probabilities, d) stationary state probabilities, e) Viterbi-decoded movement track of lobster 168.

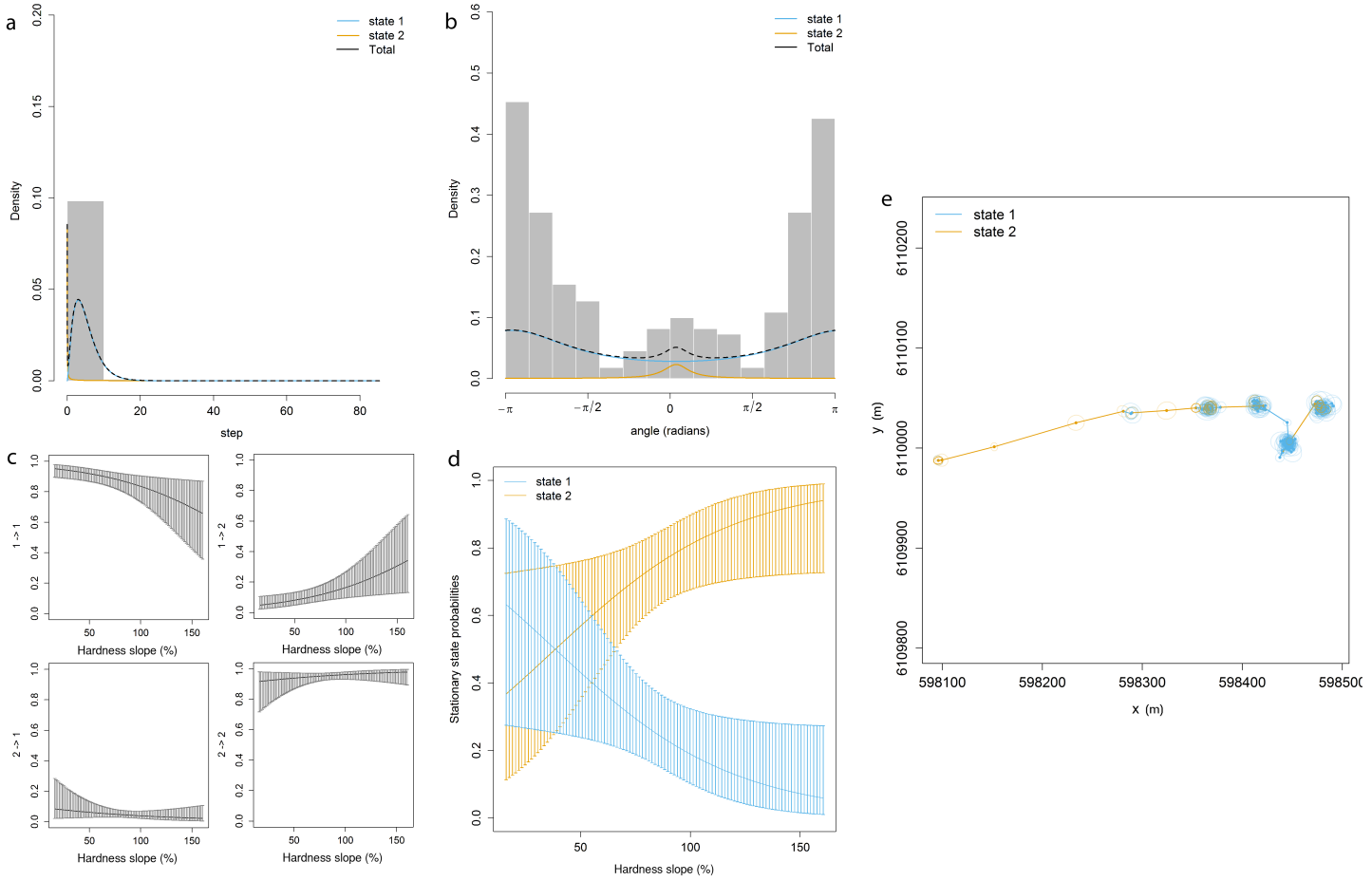

Figure 4.13: Movement process of lobster 170 as a function of hardness slope (%) using multiple imputation. Activity variable = 1.5 h and predictive time step = 1 h. a) step length distribution, b) turning angle distribution, c) transition probabilities, d) stationary state probabilities, e) Viterbi-decoded movement track of lobster 170.

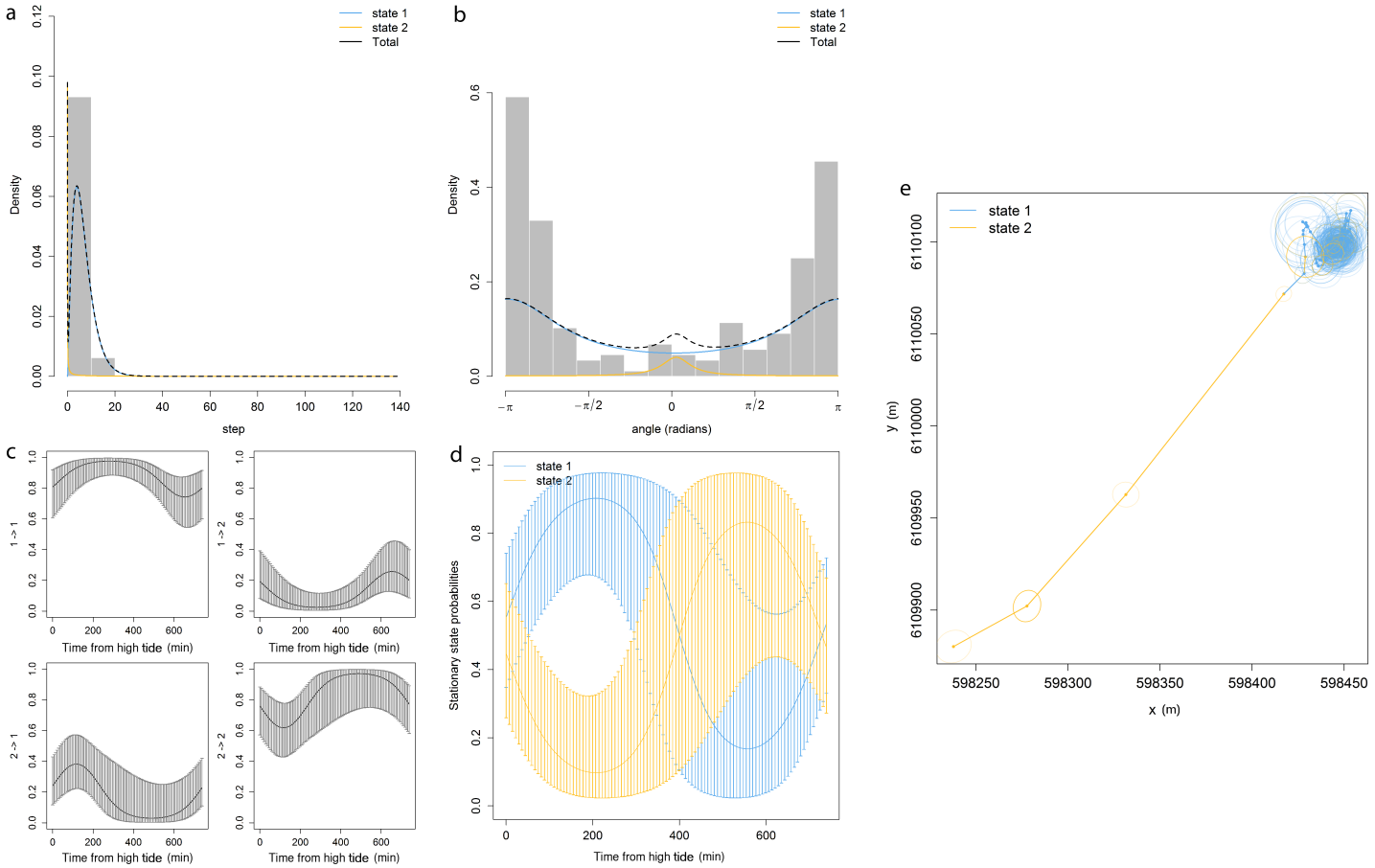

Figure 4.14: Movement process of lobster 204 as a function of time from high tide using multiple imputation. Activity variable = 2 h and predictive time step = 2 h. a) step length distribution, b) turning angle distribution, c) transition probabilities, d) stationary state probabilities, e) Viterbi-decoded movement track of lobster 204.

Table 4.4: Model estimates and associated confidence intervals for Fig. 4.11 to Fig. 4.14. Time in states is estimated as a proportion.

		State 1		State 2	
Lobster	Parameter	Estimate	CI	Estimate	CI
159	Step mean	8.38	7.49 9.27	33.19	0.50 65.89
159	Step SD	5.55	4.75 6.35	108.78	-0.82 218.37
159	Step zeromass	0.07	0.02 0.11	0.87	0.83 0.91
159	Angle mean	3.14	2.80 3.48	0.11	-0.20 0.43
159	Angle conc.	0.30	0.20 0.40	0.65	0.45 0.84
159	Time in states	0.60	0.0004 0.9998	0.40	0.0002 0.9996
168	Step mean	6.25	5.52 6.99	102.85	-277.97 483.67
168	Step SD	4.55	3.37 5.36	379.61	-1091.82 1851.03
168	Step zeromass	2.49^{-8}	-2.09^{-6} 2.14^{-6}	0.93	0.90 0.96
168	Angle mean	3.12	2.63 3.60	-0.02	-0.41 0.38
168	Angle conc.	0.24	0.14 0.35	0.70	0.401 0.99
168	Time in states	0.91	6.322^{-19} 1	0.09	6.76^{-21} 1
170	Step mean	5.14	4.47 5.80	37.08	-54.21 128.36
170	Step SD	3.31	2.63 3.98	131.92	-204.85 468.69
170	Step zeromass	0.04	0.001 0.07	0.97	0.95 0.99
170	Angle mean	-3.03	-3.52 -2.523	0.12	-0.36 0.59
170	Angle conc.	0.25	0.13 0.37	0.75	0.34 1.16
170	Time in states	0.60	0.01 0.99	0.40	0.003 0.993
204	Step mean	6.81	6.01 7.62	26.10	-39.58 91.78
204	Step SD	4.42	0.38 3.67	107.74	-170.23 385.70
204	Step zeromass	0.11	0.03 0.50	0.89	0.82 0.95
204	Angle mean	-3.10	-3.55 -2.65	0.08	-0.61 0.77
204	Angle conc.	0.29	0.17 0.42	0.72	0.11 1.33
204	Time in states	0.72	2.16^{-10} 1	0.28	3.37^{-11} 1

4.4 Discussion

Acoustic telemetry is an effective method for remotely studying animal movement in the field, and this is the first time that acoustic telemetry data have been used to explore decapod movement processes. There was evidence of different activity levels and behavioural states within the small number of lobster tracks analysed, with results supporting the findings of previous work relating lobster activity to environmental periodicity (e.g. Scopel et al., 2006; Smith et al., 1998c), and substrate (Skerritt et al., 2015; Geraldi et al., 2009). Despite acoustic telemetry providing near continuous data collection the analytical techniques used in this study highlight the ongoing challenges of studying cryptic marine organisms, such as sampling rate, missing observations and the limitations associated with data interpolation. These challenges are potential sources of bias and can complicate the biological interpretation of models.

4.4.1 Autocorrelation and missing data

The cyclical behaviour of lobsters became more apparent at larger sampling periods. Due to the sheltering behaviour of lobsters, a 5 min sampling period was chosen in order to maximise the detections of the lobsters if they were active. However, lobsters are slow moving and relatively sedentary for large amounts of time (O'Grady et al., 2001). This can result in a high error to signal ratio for movements that are less than the mean error, here approximately 4 m. The periodic use of shelters that follows a 24 h cycle is a well known aspect of lobster ecology (Scopel et al., 2006; Smith et al., 1998c, 1999, 2000). Lobsters are also known to reduce activity levels, or use shelters in response to high current speeds (Howard and Nunny, 1983); however, the current speed was not measured during the 2013 data collection. Instead a 12.4 h cycle was used to model the time from high tide under the assumption that the fastest part of the flow would be 2 h either side of high tide, but this was not significant. The aim of this analysis was to determine the effect of environmental periodicity on sheltering behaviour. It is possible that there was an effect of the tidal cycle on activity (Howard and Nunny, 1983), but that it was not sufficient to trigger sheltering behaviour, or lobsters were sheltering but the tagged cheliped was extended outside the entrance, and therefore lobsters were still detectable (Pottle and Elner, 1982).

4.4.2 Behavioural Change Point Analysis

There was evidence of both restricted and longer range directional movement using BCPA. The results of BCPA were sensitive to the choice of 'threshold' and 'cluster width'. Changes in behaviour that were identified during periods of restricted movement could be attributed to emergence behaviour; however, these could also be

spurious change points identified due to the larger error to step length ratio associated with shorter restricted movement steps (Hurford, 2009). Increasing the cluster width in an attempt to homogenise behaviour during these times resulted in changes to more directional or faster behaviour not being identified. This was probably due to the time lobsters spent undertaking directional movement being relatively short in duration compared to the amount of time they spent not moving, or moving within a restricted area (Smith et al., 1998c). These differing timescales mean that homogenous behaviour at increasing cluster width, an assumption of flat BCPA, was unlikely. The range of μ values for the flat BCPA using $log(V)$ can be explained in a similar way. The autocorrelation of $log(V)$ is likely to be highly dependent on the tidal cycle and the substrate the lobster is traversing (Howard and Nunny, 1983; Skerritt et al., 2015) and changes in speed may be observed over smaller time scales than directional persistence. Change points in $log(V)$ may therefore be better identified by using a smaller sweeping window, although smaller window sizes are less robust and would potentially identify more spurious change points during times of restricted movement (Gurarie et al., 2009).

4.4.3 Hidden Markov Models

The large number of small and zero step lengths contributed to the uncertainty and the poor modelling of the state dependent parameters, particularly the turning angle, as a result of a large noise to signal ratio (Hurford, 2009). In an attempt to address this, larger predictive intervals were chosen; however, this resulted in smaller data sets, impeding convergence, or a smaller number of transition probabilities per cycle, resulting in environmental covariates being preferred at larger predictive time steps.

The confidence intervals associated with the mean step length in state 2 were large, and as a result overestimated the proportion of time spent in state 2. The inclusion of 0 m step lengths in the state 2 distribution could be due to the larger predictive time steps used; if there were not enough positions to fully describe the restricted tortuous movements at positions where the lobster had temporarily stopped, the model could classify the movement using the near 0 turn angle rather than the short step length. This misclassification will likely have reduced the effect size of covariates and biased estimates, not only in the state dependent distributions, but also the transition probabilities. For example, the finding that lobster 168 had a higher probability of being in state 2 during the hours of 0500 and 1000 is slightly surprising. Day time movements of lobsters have been previously documented (Jury et al., 2001; Smith et al., 1999, 1998c) and may be linked to periods of reduced diurnal light levels (Smith et al., 1999). However, there was large variation associated with state 2 step lengths and large numbers of zero or near zero step lengths being included in state 2 (Table 4.4, Fig 4.12 e) many of which likely occurred during day time hours as

indicated by the results of the GEE. The inclusion of a 24 h cycle likely classified the true day time movements and day time zeros, as a result of sheltering, together in state 2, and the predominantly nocturnal restricted behaviour in state 1.

The number of behavioural states used in HMMs can be difficult to determine (Pohle et al., 2017). Only 2 behavioural states were chosen to model lobster behaviour in this study for simplicity of interpretation and due to the relatively small amounts of directional longer range movement exhibited by tagged lobsters. HMMs are not true representations of biologically relevant behaviour and it is likely that the behavioural states of lobsters are more numerous, and differences between them more subtle, than simply 'restricted movement' and 'longer range movement' (Langrock et al., 2012). HMM models can have difficulty in modelling movement processes where large amounts of small movements distances close to 0 are made, an alternative solution to this problem would be to use a hierarchical approach, modelling both a fine-scale and broad-scale movement process (Leos-Barajas et al., 2017a).

Using the lobsters' detection period to derive an activity variable is a source of bias in the current models that assume negligible and randomly distributed error (Langrock et al., 2012). It is highly probable that there were missing observations due to imperfect detection within a heterogeneous benthic environment, in addition to missing observations relating to sheltering behaviour. Missing values may be more likely to occur on hard substrate, where lobsters are also more likely to shelter. Therefore it is difficult to decipher real or behaviour-related missingness, from detection or habitat-related missingness in this case.

4.4.4 Conclusion

This study has further highlighted the variable nature of lobster movement patterns. Although there is some uncertainty around the current results, previously known relationships between environmental periodicity and activity have been linked to fine-scale movement states for the first time. Due to the infrequent occurrence of longer range movement, future studies should consider longer deployments to maximise the opportunity to observe rarer behaviours within the tagged population. Further work is required to establish if episodes of directional movement are related to increased catchability. If movement is linked to catchability opportunities may exist to quantify the proportion of the population available to the fishery at the time of fishing, or within specific habitat types.

Pinchy got dirty from chasing birds in the yard so I drew him a nice hot bath.

Homer Simpson

Chapter 5. Quantifying the effect of movement rates on trap exposure and capture probability of European lobsters

5.1 Introduction

Catchability of lobsters is known to change in relation to dynamic environmental conditions (McLeese and Wilder, 1958; Tremblay and Smith, 2001; Bannister and Addison, 1986). This change in catch could be due to the effect of these environmental conditions on the properties of the resulting bait plume (McQuinn et al., 1988), the propensity for animals to move (Howard and Nunny, 1983; Scopel et al., 2006), and therefore discover more traps (Wiig et al., 2013; Watson III et al., 2009), or both. If the effects of environmental conditions on catchability of lobsters are not fully understood, estimates of abundance, such as catch per unit effort (CPUE) may be biased as the assumption of linearity between catch and abundance is violated (Stoner, 2004; Maunder and Punt, 2004).

Lobsters are known to move less under fast current conditions in aquarium experiments (Howard and Nunny, 1983), and previous work on acoustically tracked lobsters in the field has suggested that the probability of moving may change over the tidal cycle depending on the time from high tide (Chapter 4). Understanding how these often confounding effects may influence catchability in the field is challenging, requiring spatially-explicit tracking of animals, measurement of the environmental conditions, and a potentially large sampling period that is both long enough to capture the variability in the environmental conditions, and achieve adequate captures of tagged animals.

Due to the cost of the tags required for animal tracking, studies often provide very detailed information, but only on a small number of tagged individuals. This small sample size ultimately limits the ability of studies to make the population level inference required to be useful to management (Fieberg et al., 2010). Simulation modelling provides a cost-effective framework to develop a mechanistic understanding of ecological processes and to investigate how individual level properties might influence population outcomes (Grimm, 1999; Grimm and Berger, 2016). Although it is possible to infer the effect of lobster density or distribution on catch using diver surveys (e.g. Miller, 1989; Tremblay and Smith, 2001; Watson and Jury, 2013), a simulation approach is particularly useful for cryptic species such as *H. gammarus* where fishery-independent or diver surveys are logistically

difficult (Addison and Bell, 1997).

By simulating random and non-random distributions of lobsters on the seafloor Addison and Bell (1997) were able to explore the effect of distribution on the capture process, and determine that the effect of trap saturation was more important than local depletion or the decline in bait attractiveness. Other simulation studies have investigated the effect of trap spacing on catch (*Cottus asper, Hippoglossus stenolepis* and *Anoplopoma fimbria* Eggers et al., 1982), the effect of trap interactions on the estimated trapping area (*Homarus gammarus* and *Cancer pagarus* Bell, 2001), and the effect of environmental change on population dynamics (*Panulirus argus* Butler, 2003). A particular benefit of using a simulation approach is that a conceptual model can be easily tested under different scenarios, for example, relating to lobster or trap density (Bell, 2001).

The aim of this study was to gain a greater understanding of how environmental covariates might affect catch, by investigating how the catchability of lobsters may change over time in response to changes in current speed and the size of bait plumes over the tidal cycle. Individual-based models were used to simultaneously investigate how the probability that lobsters will undertake longer range movements changes over the tidal cycle, and how this in turn affects the probability of capture throughout the trapping period (soak time). Models were parameterised using previously collected data on current speed and direction, and model outputs from Chapter 4, to investigate how the probability of capture might be linked to the lobster movement process. There were three main hypotheses: lobsters would encounter more traps, and have a higher probability of being captured, when their probability of undertaking longer range movements was highest; lobsters would be more likely to detect and approach a trap earlier in the trapping period, when the bait plume was large; and the probability of capture would be highest in low strength current conditions, using large concentrations of bait that decays slowly.

5.2 Methods

5.2.1 Model environment

The model environment was a partial differential equation (PDE) advection-diffusion model (Equation 5.1) that was coupled to the stochastic individual-based model of lobster movement (Fig. 5.1).

$$\frac{\partial c}{\partial t} + u\frac{\partial c}{\partial x} + v\frac{\partial c}{\partial y} = D\left(\frac{\partial c^2}{\partial x^2} + \frac{\partial c^2}{\partial y^2}\right) \tag{5.1}$$

where c is the concentration, advection is a velocity vector (u, v), and D is the diffusion parameter acting in both x and y directions. Diffusion process was negligible

in the model relative to advection so was set at an arbitrary low level $D = 1^{-5}$.

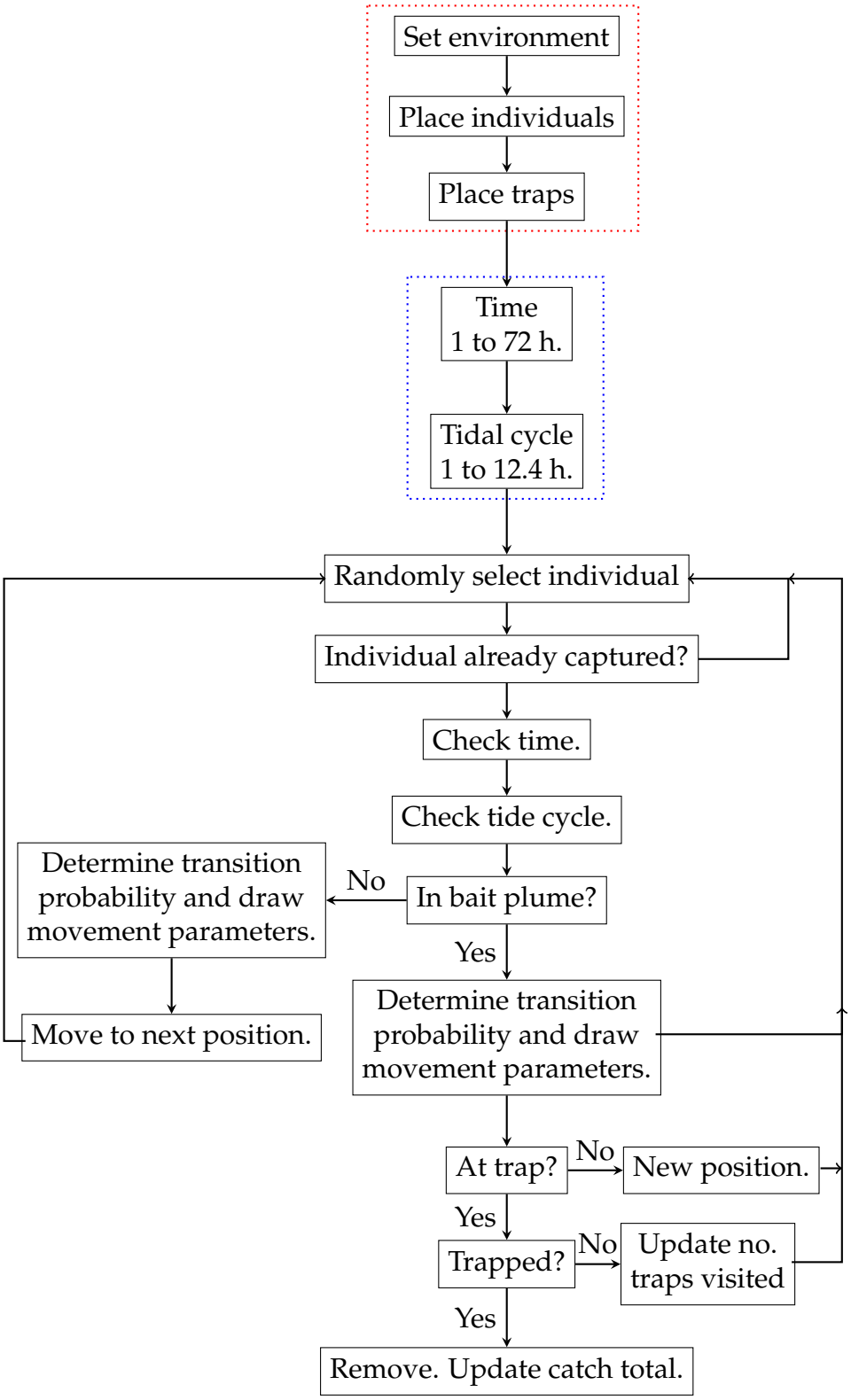

Figure 5.1: Conceptual model of lobster movement and capture process. Red dashed lines indicate the order the model environment was created and the blue dashed lines indicate the order of model time steps.

The model environment was a 200×200 grid where each cell represented 5 m. The shape and size of the bait plume was modelled through integration as a spatial 2-dimensional PDE as a function of time and current speed. The current speed was included as an advection term in the model (Equation 5.1). The bait plume was integrated over a 72 h soak period, estimated every 60 min and integrated at 6 min intervals. The ordinary differential equation model was solved using the method of lines in the R package deSolve (Soetaert et al., 2010) and the advection-diffusion model was discretised and integrated using ReacTran (Soetaert and Meysman, 2012). Advection velocity was modelled using current velocity in the x and y directions and was derived from field data measured by a current meter. The current speed was measured between 12th and 27th of May 2016 approximately 2 km off Blyth, Northumberland (55.1270° N, 1.5103° W) using a Nortek Aquadopp 3000 m current meter (current speed ranged from 0.001 - 0.415 ms^{-1}). This is an area of mixed rocky outcrops and soft substrate known to be favourable to lobsters (see Section 2.2.2). As advection velocity in the model was based on field data the speed and direction in the x and y planes changed dynamically over the course of a 12.4 h tidal cycle.

The concentration of bait left in the trap after each time step was modelled as a function of time (Equations 5.2 and 5.3, and Fig. 5.2). The initial concentration of bait S_0 decayed exponentially with time t:

$$S_t = \frac{S_0}{\exp(r_{bait}t)} \tag{5.2}$$

where S_t is the bait concentration at time t and $r_{bait}t$ is the rate of bait decline at time t. As the true rate of bait decay was not known r_{bait} can vary as a function of t_{limit}, the time that the bait drops to 20% of its original value:

$$r_{bait} = \frac{\ln(S_0) - \ln(S_0 \cdot 0.2)}{t_{limit}} \tag{5.3}$$

5.2.2 Capture rules

Traps were placed in two rows of 5 traps in the middle of the model environment. On encountering a trap the probability of capture for each lobster was modelled using the exponential decay function from Bell (2001).

$$P_{entry} = \frac{P_0}{\exp(rC)} \tag{5.4}$$

where P_0 is the initial probability of capture 0.5. The probability of trap entry P_{entry} decreases as the number of lobster caught C increases, r is instantaneous rate of change in P_{entry} defined as:

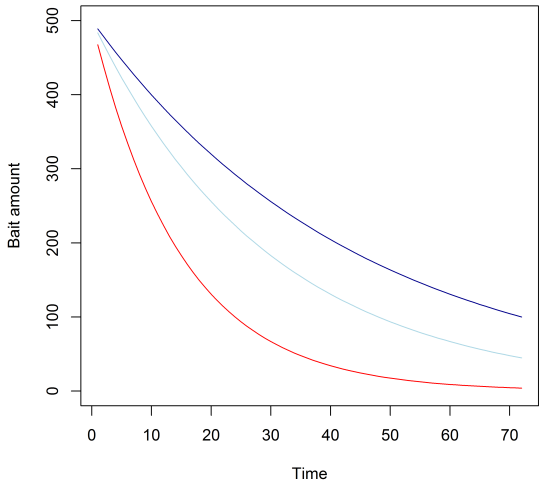

Figure 5.2: Exponential decay of S_t as a function of r_{bait} and t_{limit} when initial bait = 500. Red = 24 h, light blue = 48 h, and dark blue = 72 h.

$$r = \frac{\ln(P_0) - \ln(0.01)}{C_{0.01}} \tag{5.5}$$

where $C_{0.01}$ is the threshold catch at which the probability of capture decreases to 0.01. As in Bell (2001) C threshold was held at 5 and once captured, lobsters remained in the trap and were not available to be captured again. If lobsters encountered a trap and were not captured they were able to move randomly at the next time step and were able to visit other traps in subsequent time steps. This is different from the model by Bell (2001) that assumed this to be an unrealistic scenario; however, acoustic telemetry data (see Chapter 2) revealed multiple trap visits are possible.

5.2.3 Lobster movement model

The lobster movement model was an individual-based model run over 72 time steps to reflect a 72 h trap deployment period. Lobster movement was characterised by a step length, which was the total distance the lobster was able to move in one time step, and a turn angle, which was the direction that it moved during the time step. Lobster movement was determined by one of two movement states: state 1 'restricted movement' (Fig. 5.3a and Fig. 5.3b) characterised by short step lengths and tortuous turn angles or, state 2 'longer range movement' characterised by longer step lengths and directional turn angles (Fig. 5.3c and Fig. 5.3d). The movement state was determined by a series of movement rules (see Section 5.2.4).

Lobsters n = 1000 moved within a continuous environment i.e. if the step length exceeded the remaining space within the model environment the lobster 'reappeared' at the opposite end of the model environment. Initial lobster locations were

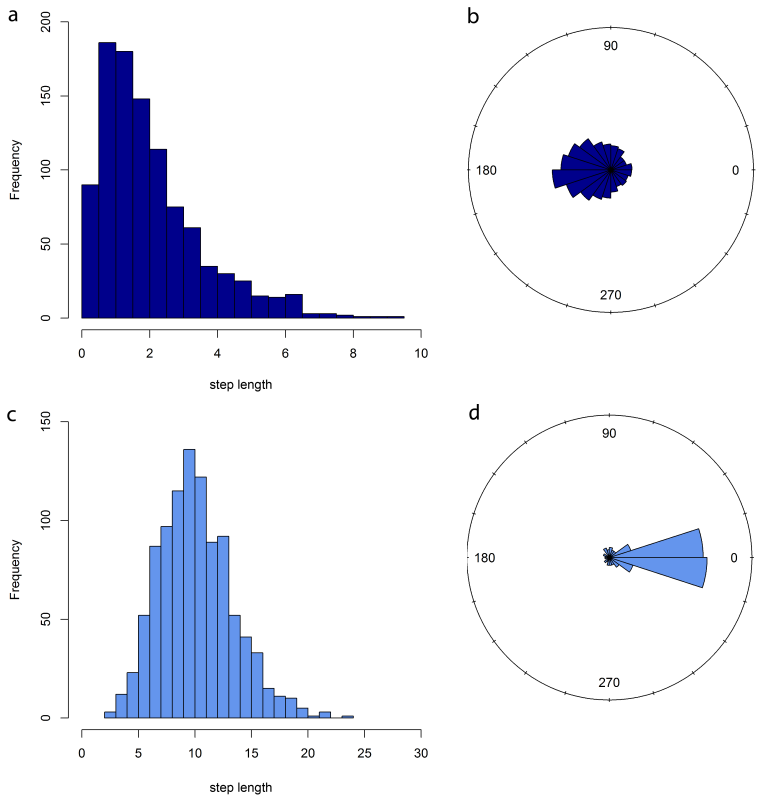

Figure 5.3: Step length and turn angle distributions for the two movement states. Dark blue = state 1 and light blue = state 2. a) State 1 step length shape = 2 and rate = 1, b) State 1 turn angle, mean = π and concentration = 0.5, c) State 2 step length shape = 9 and rate = 0.9, d) State 2 turn angle mean = 0 and concentration = 0.95.

determined randomly within the model environment; once set-up these initial conditions remained the same for the subsequent model scenarios, for example, lobster one always started at the same randomly chosen location. Lobster movement was incremental, moving 1 grid cell at a time for the duration of the step length. This allowed the lobster to interact with its environment and bait plumes that occurred between its position at time t and its new position at $t + 1$. If a lobster encountered a bait plume the distance to the trap location was calculated. If the trap distance was less than or equal to the remaining step length the lobster went directly to the trap and the probability of capture was determined by the number of lobsters already present in the trap (Bell, 2001; Addison and Bell, 1997) (Equation 5.4). When the distance to the trap was greater than the remaining step length the lobster went as far as possible and had to wait until the next time step to move again. If it was still in the bait plume then it continued towards the trap as described or, if not, it moved in the direction drawn from the turning angle distribution. Therefore, if a bait plume was encountered the probability of beginning to approach a trap was 1; however, as the lobster had to wait until the next time step to complete its approach if its remaining step length was insufficient to reach the trap, the probability of successfully locating the trap became dependent on the size of the plume area, the degree to which it moved between time steps, and the distance the plume was from the trap.

5.2.4 Movement rules

At each 1 h time step of the simulation the order in which lobsters moved was chosen at random. The movement state was determined as a function of the tidal cycle (12.4 h) and probabilities of transitioning between state 1 and state 2 (Fig. 5.3) were extrapolated from Chapter 4 Fig. 4.11 using a loess regression. Step lengths were drawn from the gamma distribution, and turn angles were drawn from the wrapped Cauchy distribution (Fig. 5.3). A conceptual model of lobster movement and the capture process is outlined in Fig. 5.1.

5.2.5 Model coupling

The bait plume model was integrated over a one hour period with a 6 min time to solution. Only grid cells that exceeded the bait threshold were classed as containing detectable levels of bait plume. The simulation bait threshold was held constant at 3 for all model runs, but a larger or smaller threshold would have resulted in a larger or smaller bait plume. Plumes were then reclassified according to the trap number from which they originated, this enabled the trap and the bait plume to remain identifiable throughout the simulation.

The plume model and the movement model were both initiated at high tide, so that transition probabilities for changing between the two movement states changed over time with the corresponding current speed (advection). Movement parameters were passed to the model at each time step so that they could be integrated over time with the relevant plume and advection conditions. Plume models were run under different conditions using unique combinations of starting values; three different values for the initial bait (250, 500, 1000), three different values for t_{limit} (24 h, 48 h, 72 h), and three different strengths of advection (0.5, 1, or 2 $\times$ the observed current speed) (Fig. 5.4).

5.2.6 Model outputs

The model outputs were the lobster's movement state at each time step (1 to 72), the x and y positions at each time step, if a lobster visited a trap (0 or 1), if a lobster was caught (0 or 1), and the ID of the trap (1 to 10) that the lobster visited or was captured in.

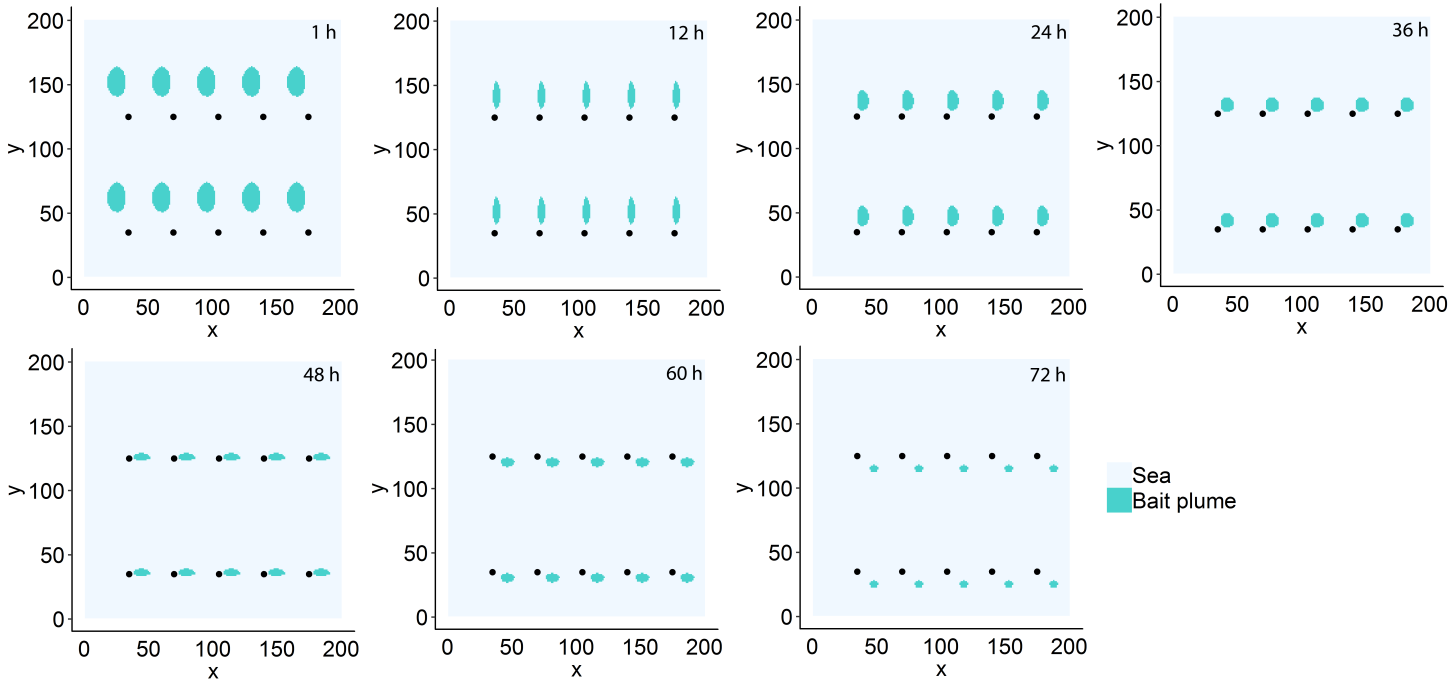

Figure 5.4: Changes in the size, shape and distance travelled by the bait plume over the trapping period. Model conditions Advection = 1, t_{limit} = 48, Bait = 500. The numbers in the top right of the figures represent the hours since the trap was deployed. Black dots = trap locations.

5.2.7 Model analysis

Simulation outputs were first analysed using a Cox proportional hazard model using R package *survival* (Therneau, 2015) to determine the relationship between the time to capture and the covariates advection, the rate of bait decay as determined by t_{limit}, the initial bait concentration, and the number of times a lobster spent undertaking long range movement. Results from the Cox model suggested that the assumption of proportional hazards was violated. Subsequently the cumulative catch over time was modelled as a function of the asymptote, xmid (the point where the catch total is half the size of the asymtote), and the scale parameter of the curves using nonlinear least-squares (NLS) implemented in the *R* package *nlme* (using *nlsList* and *sslogis*, Pinheiro et al., 2015). The resulting model coefficients were modelled as separate multiple regressions to investigate the effect of advection, bait concentration, and t_{limit} on the cumulative catch.

5.3 Results

Trap visitations followed a 12.4 h tidal cycle (Fig. 5.5a). The number of visitations per time step reduced half way through the fourth tidal cycle after approximately 42 h (Fig. 5.5); the number of lobsters caught also decreased over time. The largest proportion of lobsters that were in state 1 at the time of capture were caught in the first 6 h of trap deployment (Fig. 5.5). There was a spike in catch towards the end of the first tidal cycle 12 h, and only small numbers of lobsters were caught after the fourth tidal cycle (2nd day of deployment) (Fig. 5.5).

5.3.1 The probability of capture

The initial survival model contained all covariates; bait concentration was non-significant and was removed from the model (p = 0.96). In the subsequent model t_{limit}, advection, and the amount of time in state 2 were significant (Table 5.1); however, the hazard was not proportional with time (Fig. 5.6). A second survival analysis investigated an interaction between t_{limit} and advection, but this was non-significant (p = 0.14).

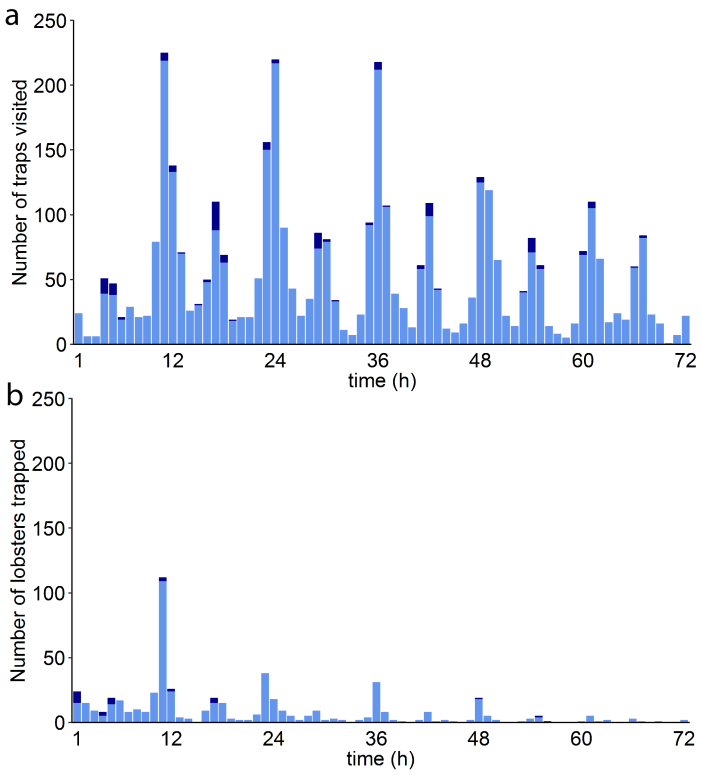

Figure 5.5: Total trap visitations and numbers of lobsters captured across all model combinations. a) traps visited, b) number of lobsters trapped. Dark blue = movement state 1, light blue = movement state 2.

Table 5.1: Cox proportional hazard model estimates.

	coef	exp(coef)	se(coef)	z	p
t_{limit}	0.006	1.005	0.002	2.46	0.014
Advection	-1.137	0.321	0.108	-10.50	< 0.001
Time steps in state 2	-0.264	0.768	0.006	-43.44	< 0.001

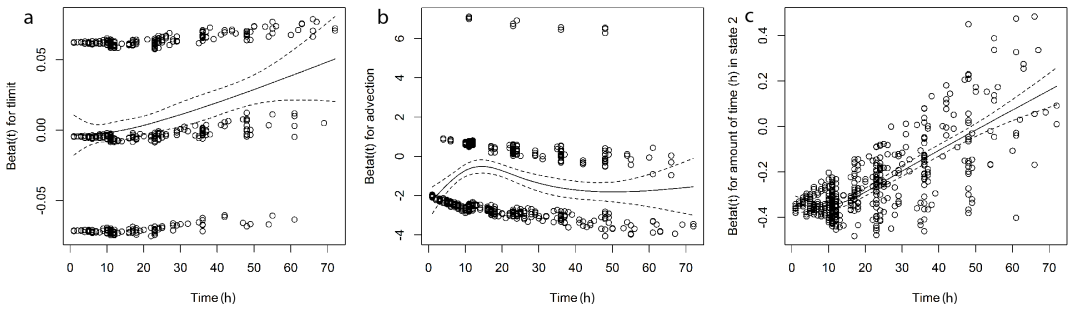

Figure 5.6: Non-proportional hazard as identified by $cox.zph$. a) t_{limit}, b) advection, c) number of time steps in state 2.

5.3.2 Model catch rate

The rate of capture was highest in the first 12-24 h for all model combinations (Fig. 5.7). The number of lobsters caught was highest when the advection was 0.5, and lowest when advection was 2 (Fig. 5.7). The numbers of lobsters caught did not differ between the 3 unique values of bait concentration (Fig. 5.7). The cumulative catch curve was first modelled as an asymptotic logistic regression using NLS (Fig. 5.8). The cumulative catch curve was modelled as a function of advection, bait concentration and t_{limit}. Starting estimates were unable to be estimated for two of the simulation models, advection = 2, bait = 250, t_{limit} = 24 and advection = 2, bait = 250, t_{limit} = 48, and these were removed from the model. There was good agreement between the fitted values from this model and the observed values from the simulation, (Fig. 5.9).

The estimates from the NLS were then modelled as multiple regressions. There was a significant effect of advection and t_{limit} on the catch curve asymptote, but the initial bait concentration was not significant (p = 0.34). The model was rerun with bait concentration removed, there was a significant negative effect of advection (β = -16.22, $p < 0.001$), and a positive significant effect of t_{limit} (β = 3.49, $p < 0.001$) on the cumulative catch curve asymptote. There was no significant effect of advection, bait concentration, or t_{limit} on xmid (advection and bait concentration p = 0.86, t_{limit} p = 0.08). There was a significant negative effect of advection on the cumulative catch scale parameter (β = -2.63, $p < 0.001$), but both the initial bait concentration (p = 0.87) and t_{limit} (p = 0.14) were not significant. The overall model fit for the asymptote model was R^2_{adj} = 0.93, and for the scale parameter was R^2_{adj} = 0.41.

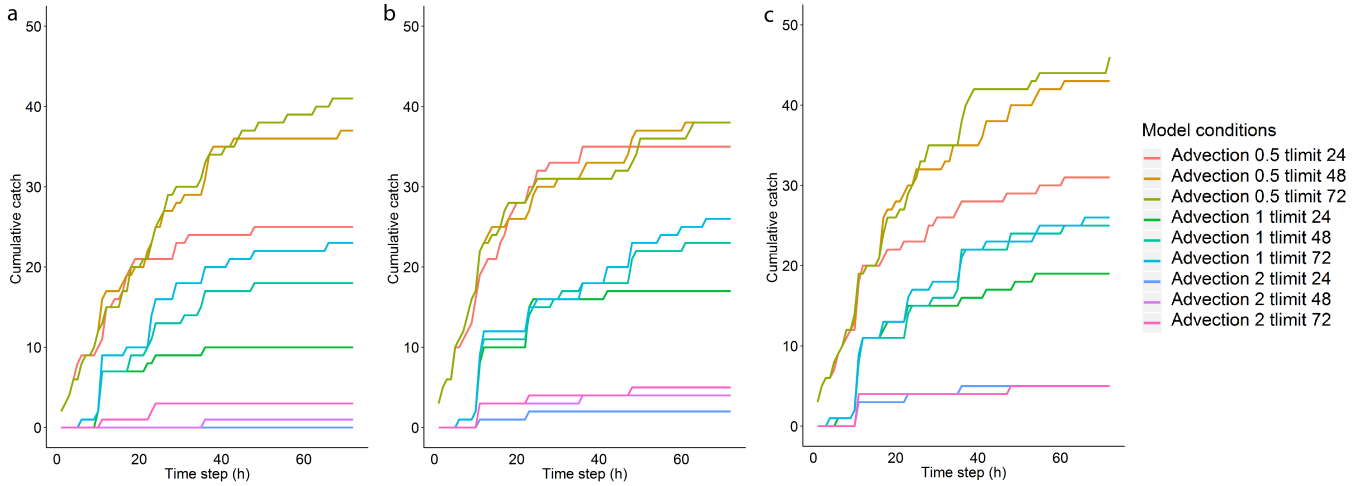

Figure 5.7: Cumulative catch curves for each of the model simulations. a) bait 250, b) bait 500, c) bait 1000. See legend for advection and t_{limit} values.

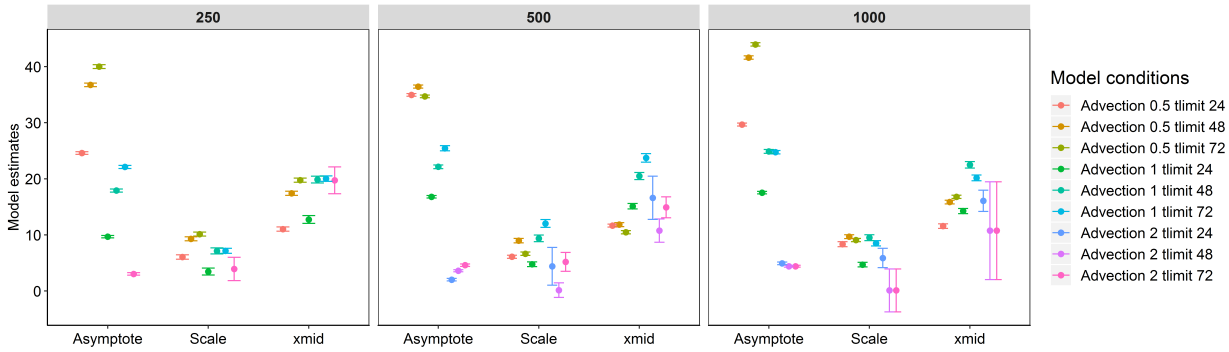

Figure 5.8: Model coefficients from the NLS analysis. The coefficients correspond to the curves in Fig. 5.7 with a corresponding legend. The numbers above plots represent the initial bait concentration.

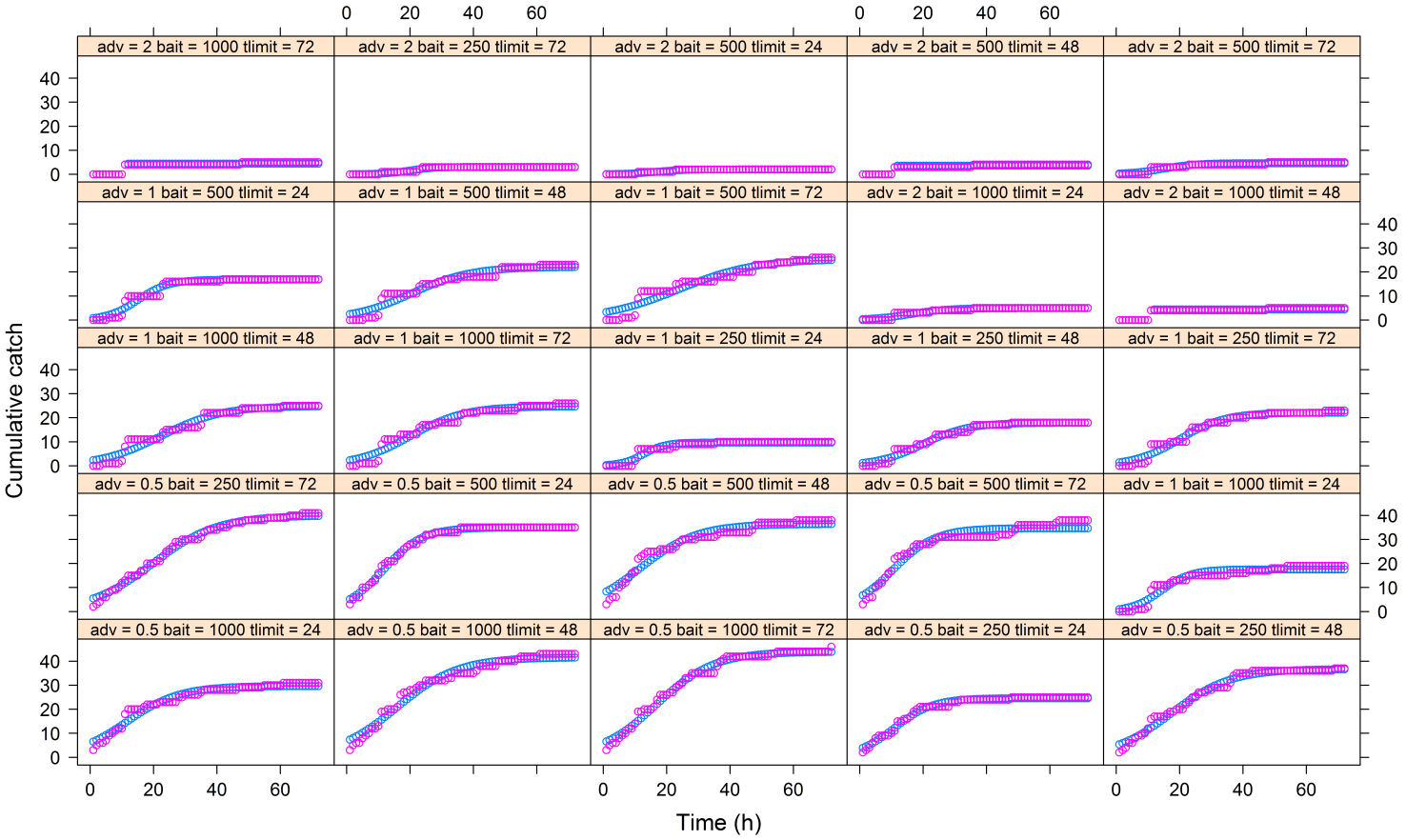

Figure 5.9: Observed and predicted cumulative catch curves for each of the model simulations. Blue = fitted values from the nonlinear least-squares analysis, pink = observed data from the model simulations.

5.3.3 Initial distance from trap

The effect of the initial distance between a lobster and the nearest trap (i.e. distance from nearest trap at t = 0) on the probability of capture was investigated as a binomial generalised linear model using the additional covariates, number of time steps in state 2, advection strength, initial bait concentration, and t_{limit}. This model was zero-inflated and was refitted using the $zeroinfl$ function from the $pcsl$ R library (Zeileis et al., 2008). However, there were still too many zeros to effectively model the relationship, and the possible impact of initial distance is discussed below.

5.4 Discussion

This study used a simulation model to investigate the effect of lobster movement in relation to the tidal cycle on the probability of capture throughout a 72 h trapping period and under different capture conditions. The largest numbers of lobsters in state 1 were caught early in the tidal cycle when the bait plumes were large and close to the trap. A previous field study found that smaller less mobile lobsters were caught earlier in the trapping period before larger more mobile lobsters were caught later (Watson and Jury, 2013). The number of lobster that were caught compared to those that just visited (i.e. arrived by were not subsequently caught) was greatest in first 3 h of the trapping period. During this time lobsters that were immediately in the trapping area at the time of deployment were caught, as indicated by the large proportion of trapped lobsters that were in state 1. The number slowly decreased over the following 6 h as the number of lobsters in the area was depleted before increasing slightly again as the tide began to move in the opposite direction and influence new lobsters. The spike in catch in the first 12 h coincides with a higher probability of being in state 2, thereby making reaching the trap in one time step more likely; it is also early enough in the trapping period that the traps have not become saturated which reduced the probability of capture. It is important to note that the precise timing and magnitude of this spike will likely change depending on the point during the tidal cycle the simulation model is initiated. The simulation model by Addison and Bell (1997) found that trap saturation was more important in determining total catch than local depletion of lobsters.

5.4.1 The probability of capture

The three significant covariates in the survival analysis, t_{limit}, advection, and the number of time steps in state 2, were all non-proportional with time. The positive effect size of t_{limit} was particularly small. The number of trap visits decreased with time, mostly likely due to the decreased size of the bait plume, but the effect is masked at larger values of advection. In other words it is not the size of the bait

plume, but the distance that the bait plume travels from the trap location, that is important. The negative effect of advection was greatest in the first 12 h of trap deployment, but approached zero towards the end of the first tidal cycle coinciding with lower current speeds, and the increased probability that lobsters will be in state 2 undertaking longer more directional movement. If the lobster was in state 2 when a bait plume was detected, they would have had a higher probability of reaching the trap in one move, even at increased distance typical of high advection conditions, due to the longer step lengths associated with state 2. The negative effect of the amount of time the lobster spends in state 2 is largest early in the trap deployment when the rate at which lobsters were caught was highest. This is because as the deployment time increases the overall size of the bait plume became smaller and more difficult to encounter. It could also be due to the effect of trap saturation on the capture probability later in the soak; however, as the density of lobsters was fixed the true effect of density dependence relative to the other covariates can not be known.

5.4.2 Model catch rates

The catch rate was insensitive to the concentration of bait in the trap. The negative effect of advection on the cumulative catch curve asymptote suggests the maximum catch is achieved at smaller values when traps are deployed in stronger currents. Under high advection conditions the plume will be smaller and farther from the trap, therefore the probability of reaching the trap in one time step, and remaining in the plume at the next time step is less likely. The positive effect of t_{limit} on the asymptote suggests that if the concentration of bait and the subsequent size of the plume reduces slowly over the trapping period the total maximum number of lobster caught is larger. The slower rate of bait decay means that lobsters can still be influenced by the trap later in the deployment; asymptotes are then reached later in the soak. The significant negative effect of advection on the scaling parameter suggests that the catch rate is slower under high advection conditions, again this is because it is generally harder to successfully reach the trap in high advection conditions.

5.4.3 Model limitations

Modelling the bait plume

The rate of advection was faster than the rate of diffusion in the PDE model, and as a result the bait plume moved a distance from the source of the trap that was dependent on the strength of the current. As lobsters had to either get to the trap in the remaining step length, or still be in the bait plume at the next time step, the probability of reaching the trap was a function of the distance the plume had travelled from the source trap. Although the probability that a lobster will approach a trap is

presumed to be a function of distance from the trap, the exact mechanism will be more complex than the simplified effect created by advection in the present model. Attempts were made to investigate the effect of initial distance from the trap, but the large number of zeros made this impossible.

The current model assumes that lobsters move straight towards a trap once in a bait plume after encountering a bait threshold. Lobsters will only respond to olfactory cues that they identify as biologically relevant and that are present in large enough concentrations to elicit a response (Derby and Atema, 1981; Page et al., 2011). However, the movement of a lobster searching for bait within a plume is unlikely to be a straight line due to changing concentrations as a result of bottom currents, turbulence and mixing (Webster and Weissburg, 2001, 2009; Reidenbach and Koehl, 2011). Therefore, the time a lobster takes to arrive at a real trap may be longer, over a larger distance, and as such, the probability of successfully arriving at the trap is potentially low. The bait plume in this model was a function of time and current speed and as a result the bait plume was further from the trap in strong current conditions. Therefore arriving at the trap successfully was still a function of the distance from the trap (Bell, 2001; Addison and Bell, 1997). Furthermore the lobster was required to still be in the bait plume at the next time step if it was to continue its movement towards the trap. This approach may lack the realism of some previous studies that have specifically addressed the complexities of bait-searching behaviour (e.g. Vabø et al., 2004), but the purpose of this simulation was to model the probability of capture as a function of lobster movement, current speed, bait concentration, and the rate at which bait decays, not fine-scale olfaction.

Trap saturation (Bennett, 1974) and interaction between traps (Smith and Tremblay, 2003; Bell, 2001) are important density dependent processes that can affect the probability of capture. The simulation model in this study included trap saturation by reducing the probability of capture after a catch threshold was reached (Addison and Bell, 1997; Bell, 2001). However, all traps in the simulation were considered independent of each other and none of the bait plumes overlapped. The assumption of trap independence and non-overlapping bait plumes simplified the identification of plumes between time steps and reduced the run time of the models, but is an area for future development.

The probability of lobsters transitioning from state 1 to state 2 followed the tidal cycle as estimated in Chapter 4, but did not change in relation to the changing strengths of advection i.e. 0.5, 1, or 2 $\times$ the current speed. In reality it is likely that the probability of moving would change in response to a smaller or larger range of current speeds (Howard and Nunny, 1983). For example, in overall lower current speeds (advection = 0.5) lobsters may be less constrained in their movements and the patterns observed in this study may be less pronounced.

In this model all lobsters move only in relation to the tidal cycle, other sources of environmental periodicity, most noticeably the 24 h cycle (Smith et al., 1998c, 1999, 2000), are not included. It would be possible to model this cycle either as a separate model to compare the effects of both tidal and day-night cycles on the numbers of lobsters caught, or as a joint probability. Currently the model only contains lobsters, but could be easily adapted to include crabs (Bell, 2001). Again these are areas for possible future work.

5.5 Conclusion

A particular strength of this modelling approach was that the shape of the bait plume, and the relationship between the capture probability of a lobster and its distance from the trap, did not have to be estimated as in previous studies. As a result they were able to change dynamically with the current speed and bait concentration over time, thereby including multiple aspects of the catch process in one model. Further modifications are possible to improve the realism of the model, such as additional drivers of movement, or individual variability. In its current form the model demonstrates a possible framework for testing the effects of multiple dynamic environmental processes on the probability of capture, and is of broad interest to fisheries management where a greater understanding of the effects of environmental drivers of catchability is required.

If you believe in yourself, others will believe in you...

Pepe the King Prawn

Chapter 6. Discussion

The focus of this thesis was to address knowledge gaps relating to the behavioural and spatial ecology of *H. gammarus*, and to infer how behavioural differences between lobsters may affect catchability. This work has offered new insight into how acoustic telemetry data can be used to study lobster movements and behaviour in the field, in particular the benefits of the increased realism that field studies can offer (Chapter 2). As the accuracy and miniaturisation of marine telemetry equipment has improved, techniques that have been commonly used within the terrestrial environment are now able to be used within the marine environment to infer space-sharing that would only have been previously possible via SCUBA surveys (e.g. Karnofsky et al., 1989a; Moland et al., 2011b) (Chapter 3). The naturalistic conditions and unconstrained movement of lobsters that field studies can offer are often a trade off between the experimental control that can be achieved in aquarium or mesocosm studies (Watson III et al., 2009). Where uncertainty can arise from measurement error or missing data (Chapter 4), greater understanding of the mechanistic processes that may drive movement can be achieved using simulation studies (Chapter 5). Many of the approaches used in this thesis have not previously been attempted for *Homarus* lobsters. They have offered further insight into the opportunities and difficulties associated with studying lobsters in the field, and a new perspective on how acoustic telemetry could be used to fill the knowledge gaps within lobster fisheries.

6.1 The importance of studying lobsters in the field

Previous studies undertaken in aquariums (Karnofsky and Price, 1989a; Shelton, 1981; Moore et al., 1991) and mesocosms (Watson III et al., 2009; Scopel et al., 2009) have not been of sufficient spatial scale to fully describe the movement patterns of *Homarus* lobsters. Acoustic telemetry provides a method for studying lobster behaviour in the field, and with careful consideration can be used to undertake experiments relating to behaviour in the vicinity of a trap. Distinguishing non-random from random behaviour can be difficult (Watson III et al., 2009), but there are well-established statistical techniques available to test these differences (Gotelli and Graves, 1996), if suitable behavioural metrics are derived from the tracking data. The variability in the distance that lobsters approached traps in Chapter 2 was larger than previously observed in a mesocosm (Watson III et al., 2009), but within the range of other similar

species (e.g Skajaa et al., 1998; Jernakoff and Phillips, 1988); and it is therefore likely that investigating catchability in the field can give more accurate estimates of the maximum distance of attraction. In addition to providing increased space, field experiments also capture the effect of dynamic environmental conditions reflective of those experienced by the population (Cote et al., 2018).

Watson III et al. (2009) derived the size of the effective trapping area in their mesocosm study by assuming a circular bait plume. Although the bait plume modelled in Chapter 5 was a simplified version of the true process it illustrates clearly that at sites with a highly directional current, as in this study, an assumption of a circular bait plume is not valid (McQuinn et al., 1988). If current speed and turbulence data were collected at a higher spatial resolution, bait plumes could be modelled in greater detail. These models could then be used to validate the observed distances that lobsters approached the traps. Due to the behavioural interactions associated with traps (Richards and Cobb, 1983; Miller, 1990; Bennett, 1974), diver surveys still provide the most accurate estimate of lobster density in the field, although detection of well concealed lobsters can be difficult. These dive-based surveys of lobster density could be used along with the validated bait plumes to give an estimate of the area of bait influence in the field under dynamic tidal conditions. Additional experimental work could further investigate non-random movement by fixing the location of bait sources over a longer time period to assess the impact of known locations and movement paths on capture probability.

Lobsters are known to move in relation to environmental periodicity (e.g. Scopel et al., 2009; Tremblay and Smith, 2001; Howard and Nunny, 1983). Findings from Chapter 4 suggest that while day-night cycles affect activity levels (Scopel et al., 2006; Smith et al., 1998c, 1999, 2000), i.e. undetected (sheltering) vs detected (not sheltering), the 12.4 h tidal cycle may be influential in driving changes in movement patterns (Howard and Nunny, 1983). If the effect of current speed on movement and catchability changes over the tidal cycle, as simulated in Chapter 5, then the potential bias created by unequal soak times, typical of fishery data could be amplified by the stage in the tidal cycle in which the traps are deployed. As both the distribution of lobsters and fishers is non-random (Galparsoro et al., 2009; Wahle and Steneck, 1992; Wahle, 1992b; Turner et al., 2013), and current conditions are likely to vary between local sites and geographic regions, how the capture process changes over the tidal cycle could be a source of regional variability and subsequent uncertainty in catch estimates (Stoner, 2004; Maunder and Punt, 2004). The simulation framework developed in Chapter 5 has the potential for further development and could provide a method for fisheries managers to explore catch under different dynamic conditions appropriate to their region. Further work is necessary to investigate the effect of the tidal cycle on catch rates compared to that of trap saturation.

Findings from Chapter 3 underlined the clumped distribution of lobsters in relation to suitable habitat (Galparsoro et al., 2009; Wahle and Steneck, 1992; Wahle, 1992b), and provided additional insight into their distribution in relation to other tagged lobsters. As in Chapter 2 the distances moved by some individuals were larger than those achievable in a mesocosm study (Watson III et al., 2009; Scopel et al., 2009). An obvious shortcoming of this approach is that behavioural interactions can only be assessed in relation to other tagged lobsters. It is this clumped distribution of lobsters, driving the non-random distribution of fishers, that can make accurate estimates of fishing effort from fishery data problematic (Walters, 2003). Although only a small proportion of the population were tagged in this study, the methods used in Chapter 3 could be useful in understanding the spatial distribution of different sizes and sex of lobsters, if a wider range of sizes were tagged in the future. This information would be useful to fisheries models where the assumption of spatial coverage of the population is assumed constant, such as the currently used length-based analyses (Cefas, 2017).

An acoustic telemetry array deployed at a single site can not fully describe the relationship between available habitat, lobster movement, and fishing effort, that is required to better understand the temporal changes in distribution and catchability needed to improve population estimates (Miller, 1990). An acoustic telemetry study run in tandem with a mark-recapture study using persistent T-bar tags could provide additional information on the presence of individuals within an area, perhaps allowing for the distances moved between the acoustic and marked individuals to be compared to better infer population-level movement. Although this would save money on acoustic tags, and mean that individuals outside the array still provided information on distance travelled, mark-recapture studies are labour intensive, and costly in terms of boat days, and may not be cost-effective. It is important to consider that there is likely a proportion of lobsters, due to individual-level traits, that are invulnerable to trapping (Karnofsky and Price, 1989a), and therefore regardless of tracking or marking method, if study lobsters are caught using traps then inference is biased towards the trappable proportion of the population.

6.2 Tracking technology, data availability, and lobster movement

It is an ongoing challenge to correctly identify the scale at which tagged animals are responding to their environment, particularly when outcomes of analyses may be dependent on the spatial or temporal scale (Scales et al., 2017; Benhamou, 2014). The substrate data used in this study was 5 m in resolution, although this may be considered high resolution it is likely lobsters are operating at a finer-scale and in response to features not captured by the Olex system. This may explain the limited role substrate played in explaining the lobster movement process. When substrate

was favoured in the hidden Markov models (Chapter 4) it was the variability associated with the surrounding measurements that were selected suggesting mixed substrate or edge habitat as most important for movement (Skerritt et al., 2015; Geraldi et al., 2009). The reduced significance of environmental periodicity at increased predictive intervals in Chapter 4 highlights the importance of the sampling rate and study duration when investigating the effects of dynamic environmental conditions (Scales et al., 2014). The potential importance of the tidal cycle on catchability (Chapter 5) may become more pronounced during spring tides, but as these only happen once a fortnight several months of tracking would be necessary to achieve adequate information. Prolonged tracking in an active fishery close to a busy port, similar to the study site used in this thesis, is challenging: equipment may go missing or be moved (intentionally or accidentally); competing traps may be set on top of carefully placed geo-referenced ground lines; and tagged lobsters may be fished out. Financial incentives have the potential to prevent or protect against some of these issues, but it is not feasible in the long term and outwith the budgets of many PhD studies. They also do not protect against nature-based setbacks, such as lobsters moulting out their tags, or moving out of the array (always intentionally, never accidentally). Equipment loss and sabotage were not a problem for this study, but only a small number of lobsters responded to traps in Chapter 2, limiting the population-level interpretation.

Lobsters are generally slow moving (O'Grady et al., 2001) and a longer delay between tag transmissions would have reduced the noise to signal ratio; however, their association with shelter-providing habitat requires that data are collected at high-resolution to detect their infrequent movements. Sub-setting data to achieve a longer time interval is possible, or predicting at larger time intervals as in Chapter 5; however, it is not fully understood how the change in temporal scale affects the interpretation of the movement process (Rooney et al., 1998; Scales et al., 2017). Although the short sampling delay created a large error associated with short step lengths it was not short enough to capture the back and forth movements that characterise the early escalation of aggression important in lobster behaviour (Karnofsky and Price, 1989b), limiting the biological interpretation of interactions in Chapter 3. The sampling rate is a trade-off between the multiple spatial and temporal scales at which movements, and behaviours occur. There is the possibility that accelerometers could provide additional information on lobster activity at the time of the interaction. Jury et al. (2018) indicate that activity levels recorded by accelerometers may reflect distance travelled, but additional studies in the aquarium and field investigating sampling rates, sampling period, an important consideration for Vemco style transmitting tags (Taylor et al., 2013), and attachment method would be necessary before behavioural inference was possible. Finer-scale acceleration data would be achievable with a standard stand alone accelerometer;

however, the size of the tag necessary for data storage, and retrieval of the tag from the field would be problematic. A more useful improvement in the short to mid-term would be to gather behavioural observations in addition to an acoustic telemetry, or to integrate a movement study with a mark-recapture study to infer what other individuals are present in the area. The presence of non-tagged individuals is unknown and therefore their effect on others can not be studied; this is a limitation to inferring behaviour in many tagging studies, but particularly those that can not ground truth observations due to logistical challenges.

The data used in this thesis are inherently irregular due to the sheltering behaviour of lobsters, this behaviour-related missingness was in addition to detections that were also missed while lobsters were moving. As missing detections were more likely on hard substrate where lobster were also more likely to shelter the causes of missing observations were confounded and difficult to interpolate. Analytical techniques that explicitly state that they are robust to missing data (e.g. Gurarie et al., 2009; Auger-Méthé et al., 2017; Johnson et al., 2008) are developed in response to technological short-comings, such as limited contact with satellites and large positional error (ARGOS and geolocators), or coarse tracking due to a need to maximise battery life. Often the type of missingness can be inferred using appropriate covariates; however, as previously stated detection and behaviour were confounded in this case. This inability to correctly differentiate between these two drivers of missingness was a major source of uncertainty and bias when modelling the lobster movement process. Although substrate hardness values generated by the Olex system were correlated with higher level habitat data (Skerritt, 2014), habitat-level data may have provided greater insight into the underlying structure of the substrate rather than just its hardness that would have been useful throughout the approaches used in this thesis. More accurate estimates of the utilization distribution and overlap in Chapter 3 may be achieved using a weighted approach recently developed specifically for missing and temporally irregular data (Fleming et al., 2018; Winner et al., 2018).

There was a large amount of uncertainty associated with the model estimates from the HMMs in Chapter 4. The large error to signal ratio for slow moving animals is not an easy one to solve and there are additional technological and methodological improvements that are necessary. Alternative approaches to modelling the movement process using HMMs would have been to model movement as a time to event analysis using an ordered multiple events Cox proportional hazard model. This would have involved defining the two movement states rather than estimating them, and including covariates to investigate the probability of being in one of n defined movement states. For example, a movement could be defined as a step length greater than one standard deviation, i.e. moved verses not moved, or movements could be more than two categories, not moving, moving within a restricted area, and moving longer distances. There are two approaches which can be used to model multi-state

processes: the Andersen-Gill approach where all events are assumed to be independent; and the conditional approach where probability of event 2 happening is conditional on event 1 having happened (Prentice et al., 1981).

6.3 Future work

In order to understand a catchability bias linked to sex or life history it is necessary to understand the ecological processes that are linked to these potential differences in behaviour (Stoner, 2004). The spatial and temporal scale of this study was limited, and although there were a reasonable numbers of lobsters tagged, only a small proportion responded to traps, remained in the study area, or exhibited the behaviour of interest (i.e. longer range movement in Chapter 4). An obvious improvement would be to increase the spatial coverage and the duration of the study; however, this would come at an increased cost in both equipment and boat days for what may only result in a small increase in sample size. If additional resources were possible an integrated, multiple scale approach to studying lobster movement and behaviour may provide more information (e.g. Cote et al., 2018, snow crab *Chionoecetes opilio*). The acoustic telemetry array used in this study produced data on fine-scale movement, but some lobsters did move outside the area and further information was not available on their whereabouts. By varying the configuration of the array it would be possible to gather data on both fine and coarser longer scale movements; smaller VPS arrays could be deployed on multiple areas of hard reef substrate, and presence-absence hydrophones in a linear array could be deployed to provide data on coarser scale connective movements between study areas. Coupling an acoustic telemetry study with a mark-recapture study could also provide information on longer range movements and connectivity, and field effort could be reduced if records of marked individuals caught by fishers were utilised (Cote et al., 2018). The majority of the Northumberland lobster fishery consists of a number of small private enterprises, where fishers operate within self-identified territories (Turner et al., 2013). An integrated multi-scale study within the region would offer the opportunity to study the spatial relationship between fisher effort, catch, and lobster movements.

It's not always what you say that matters, sometimes it's what you don't say.

Mr Krabs

Appendix A. Appendices

A.1 Chapter 4: Additional BCPA outputs

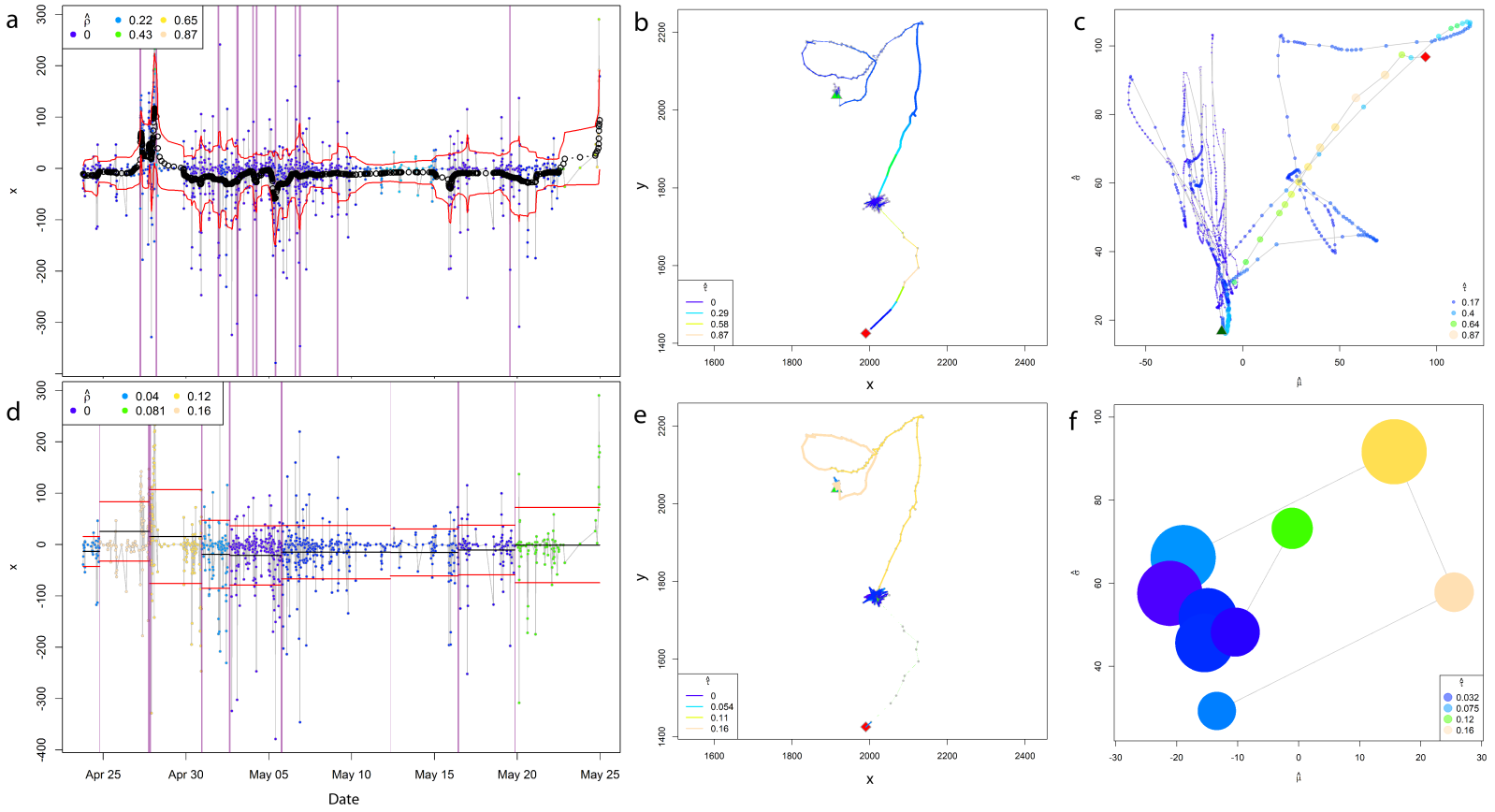

Figure A.1: BCPA analysis using the persistence velocity (Vp) of lobster 159, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 159 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 159 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

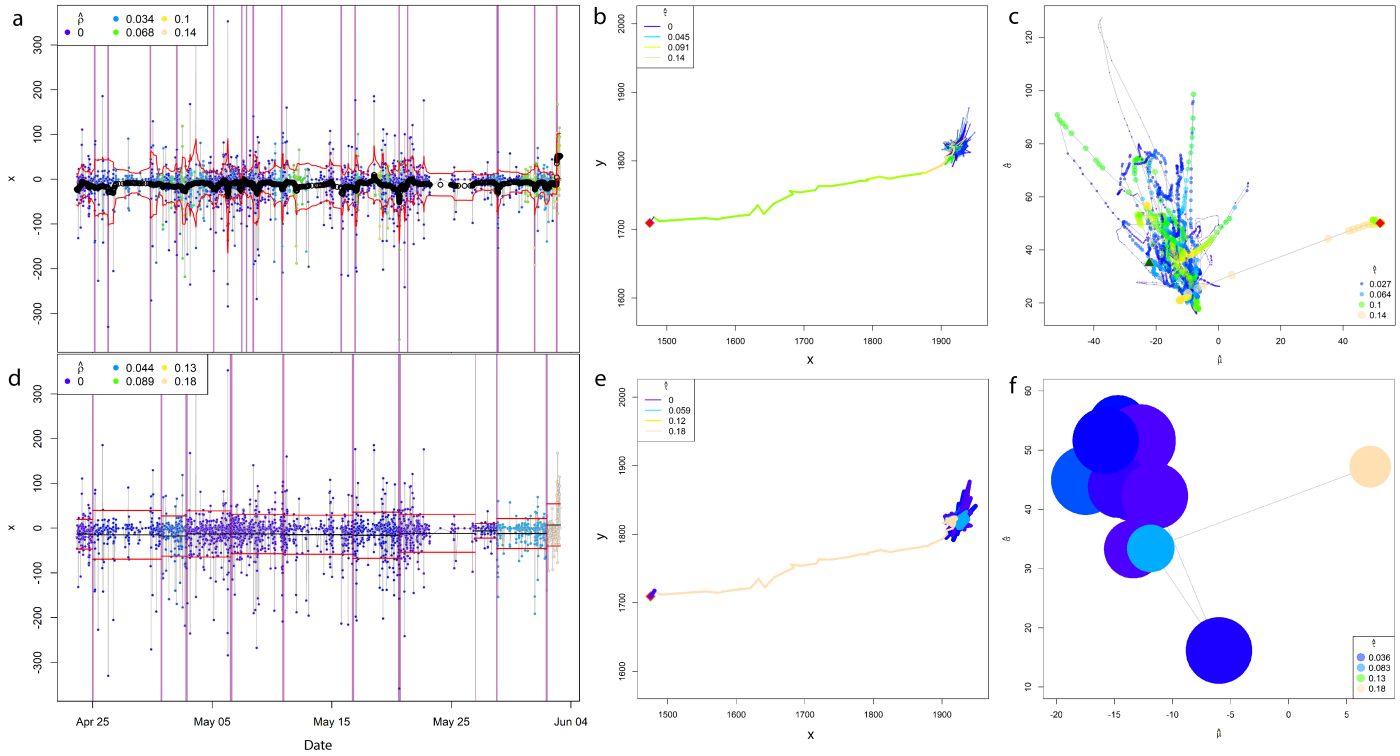

Figure A.2: BCPA analysis using the persistence velocity (Vp) of lobster 165, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 165 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 165 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

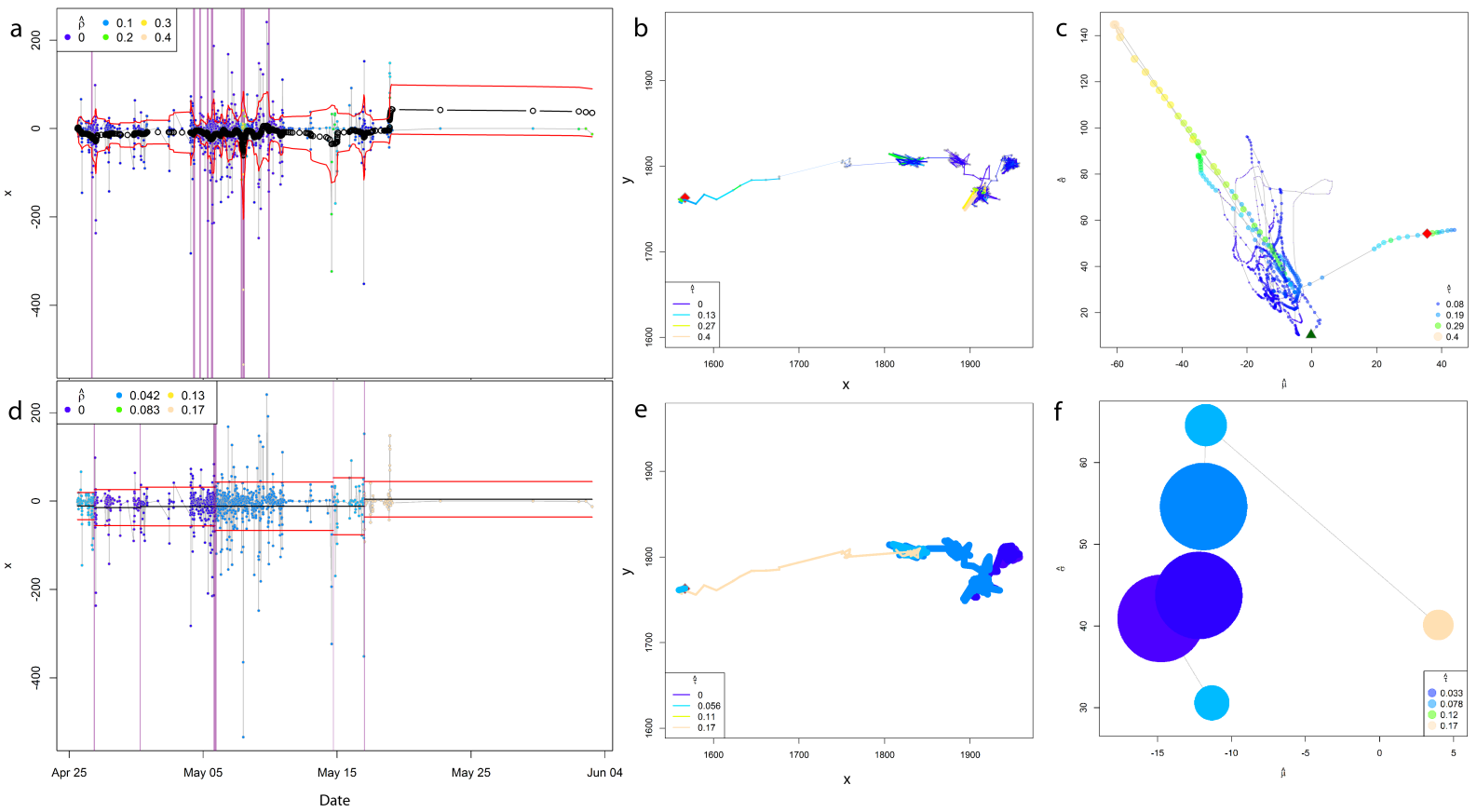

Figure A.3: BCPA analysis using the persistence velocity (Vp) of lobster 170, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 170 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 170 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

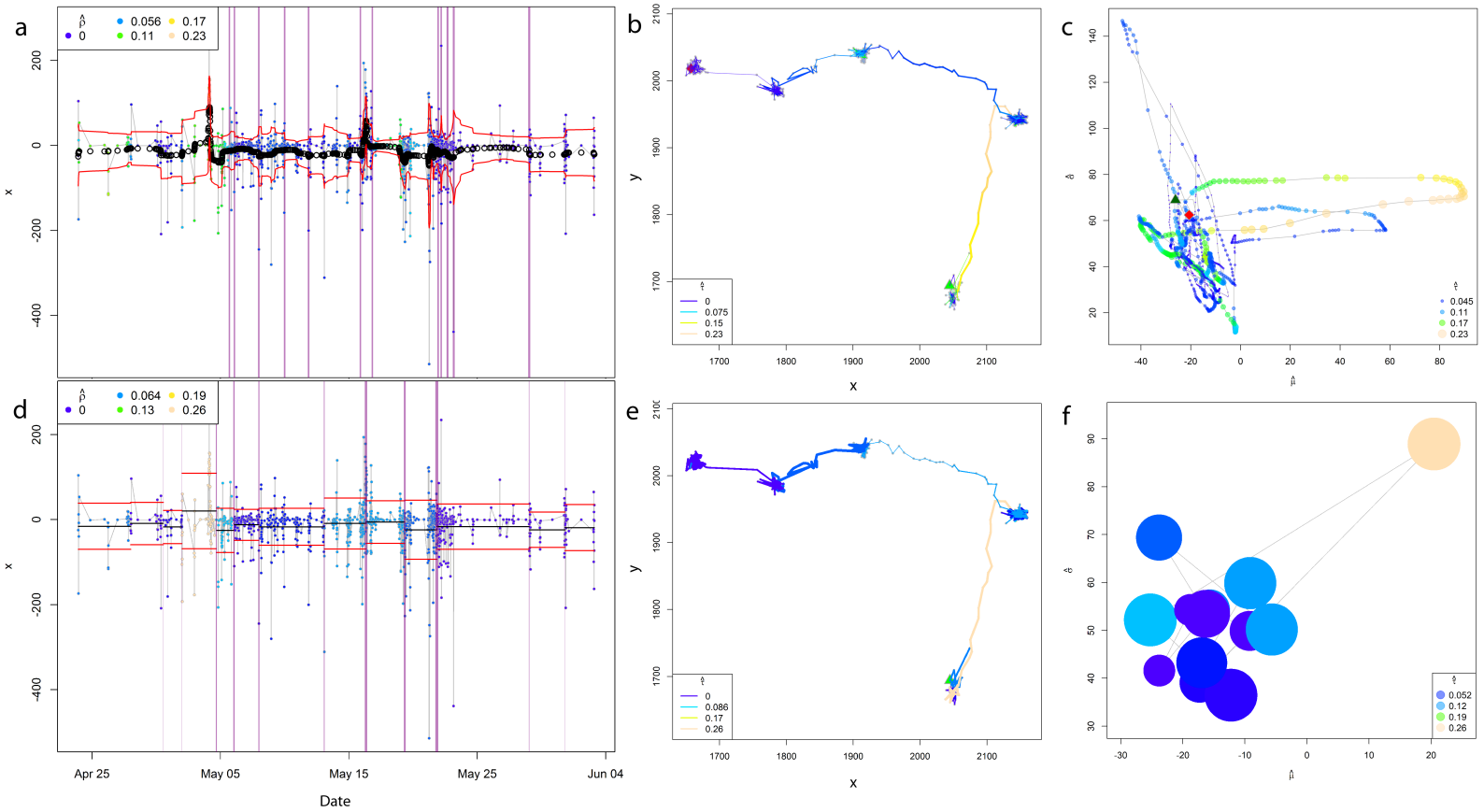

Figure A.4: BCPA analysis using the persistence velocity (Vp) of lobster 194, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 194 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 194 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

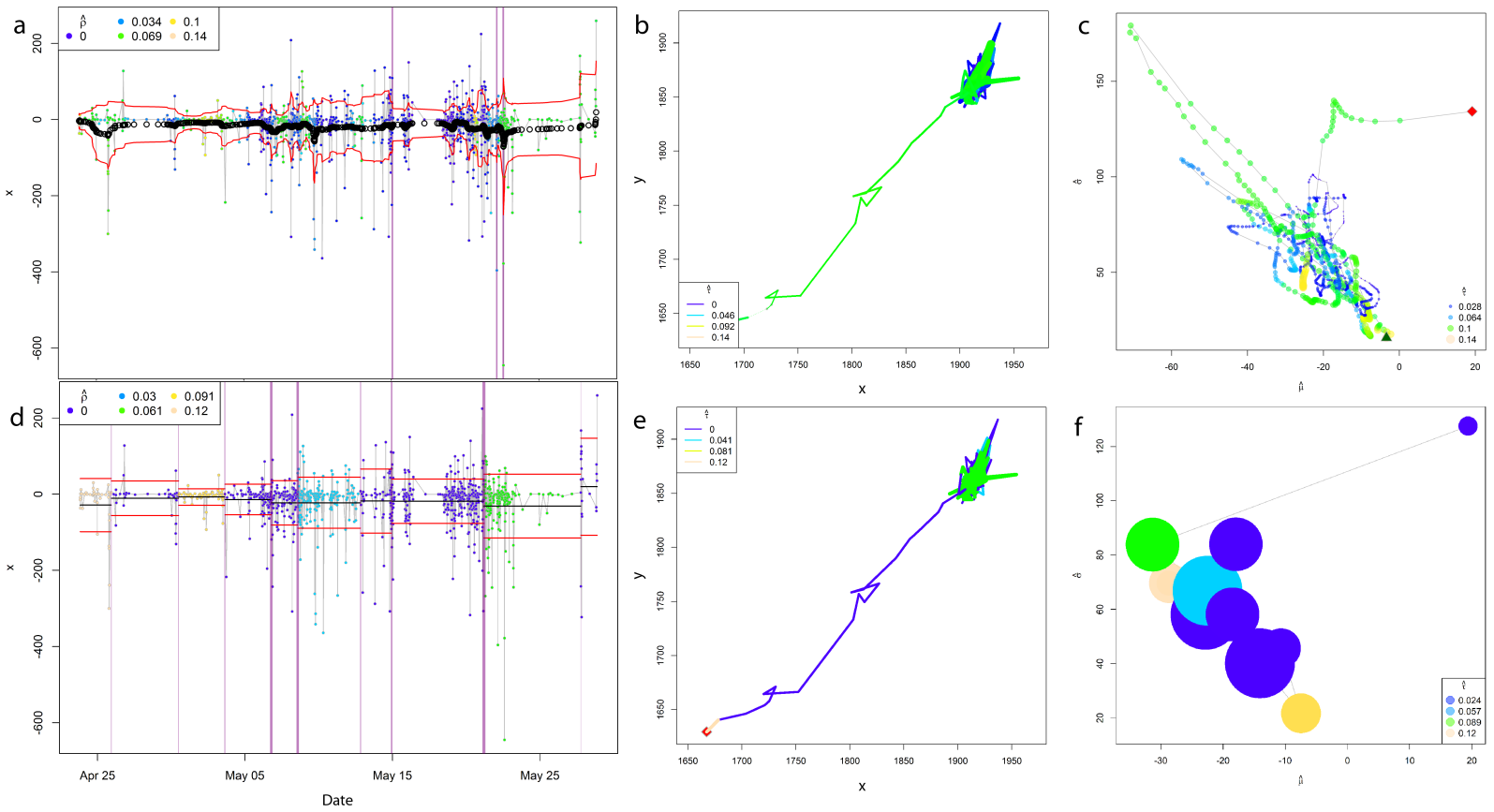

Figure A.5: BCPA analysis using the persistence velocity (Vp) of lobster 204, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 204 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 204 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

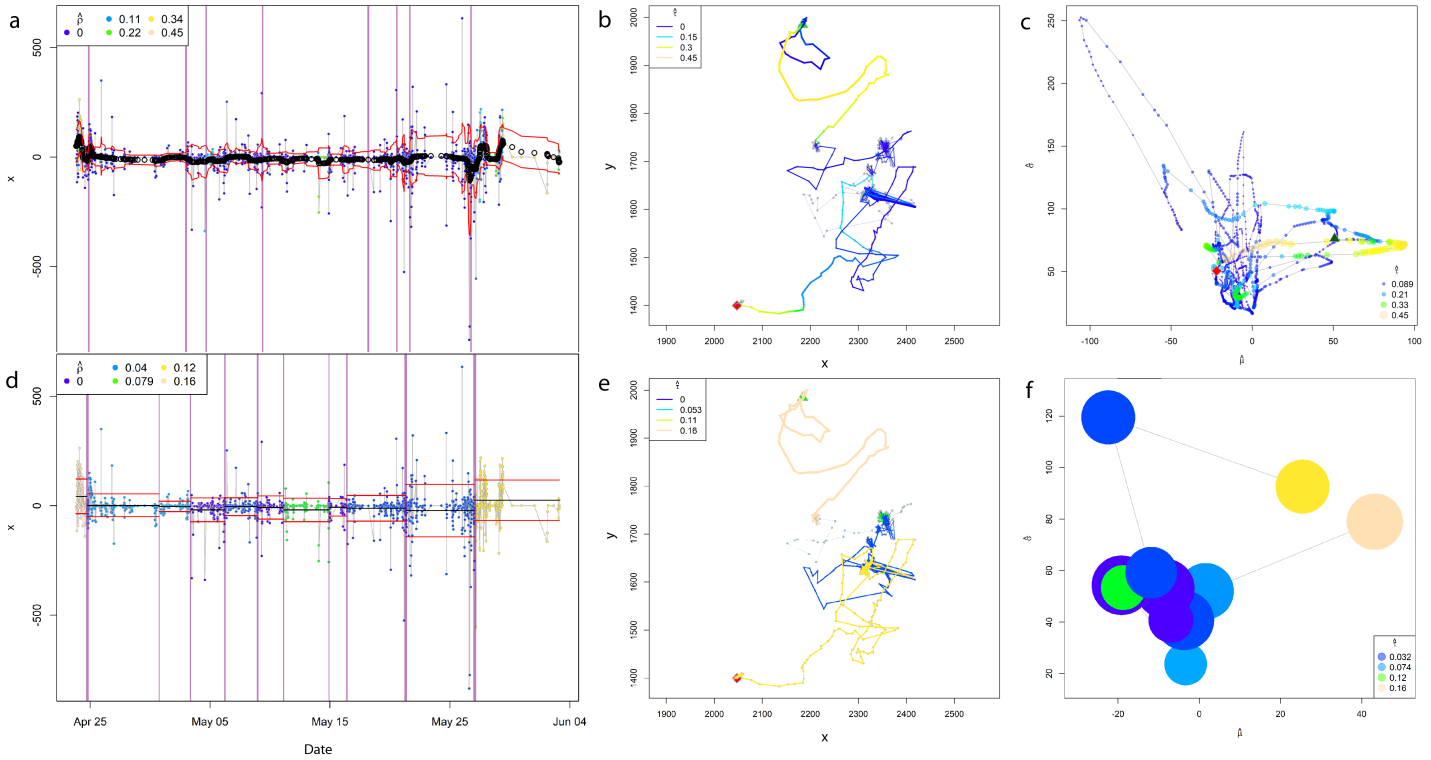

Figure A.6: BCPA analysis using the persistence velocity (Vp) of lobster 214, $K = 4$ a) smooth BCPA analysis, b) trajectory of lobster 214 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 214 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

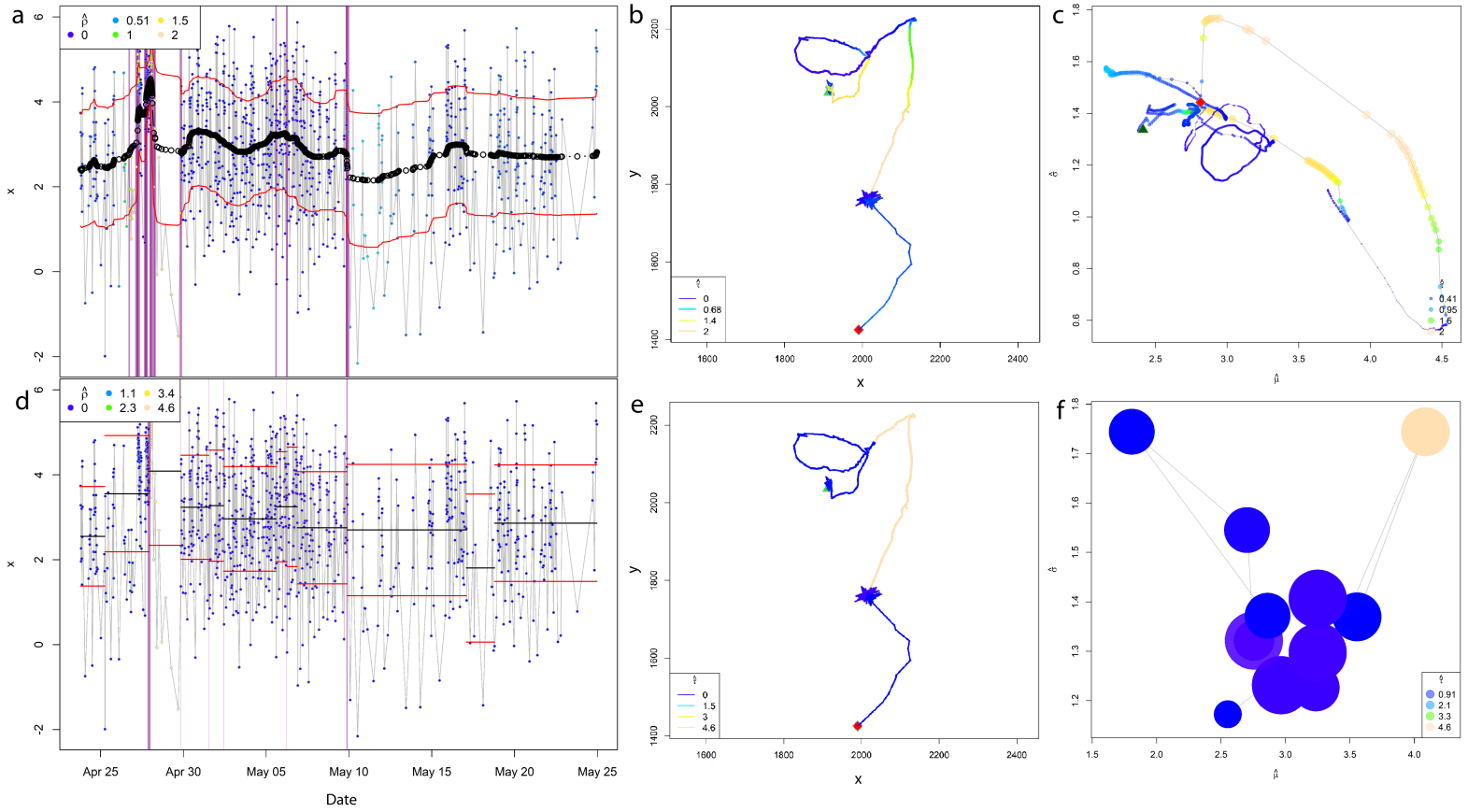

Figure A.7: BCPA analysis using the log velocity $log(V)$ of lobster 159, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 159 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 159 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

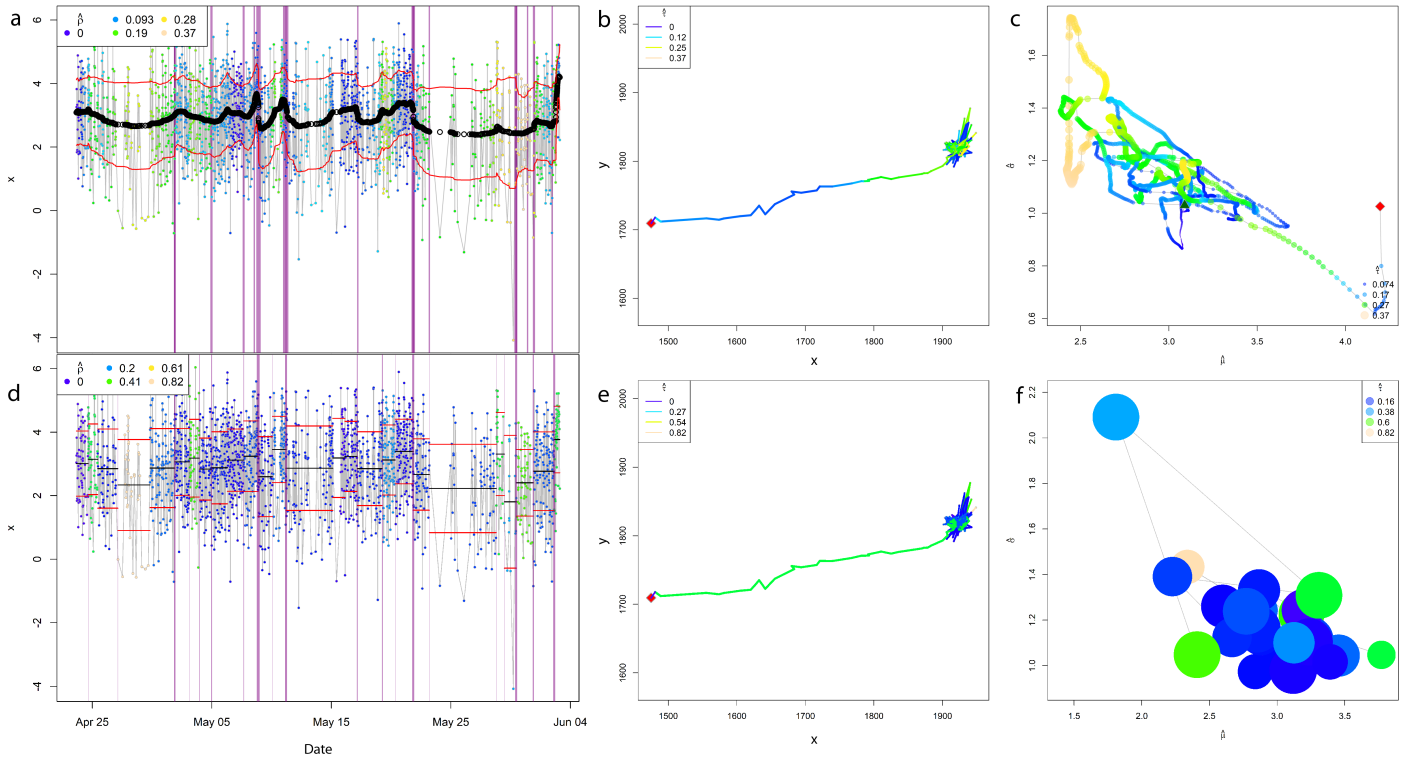

Figure A.8: BCPA analysis using the log velocity $log(V)$ of lobster 165, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 165 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 165 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

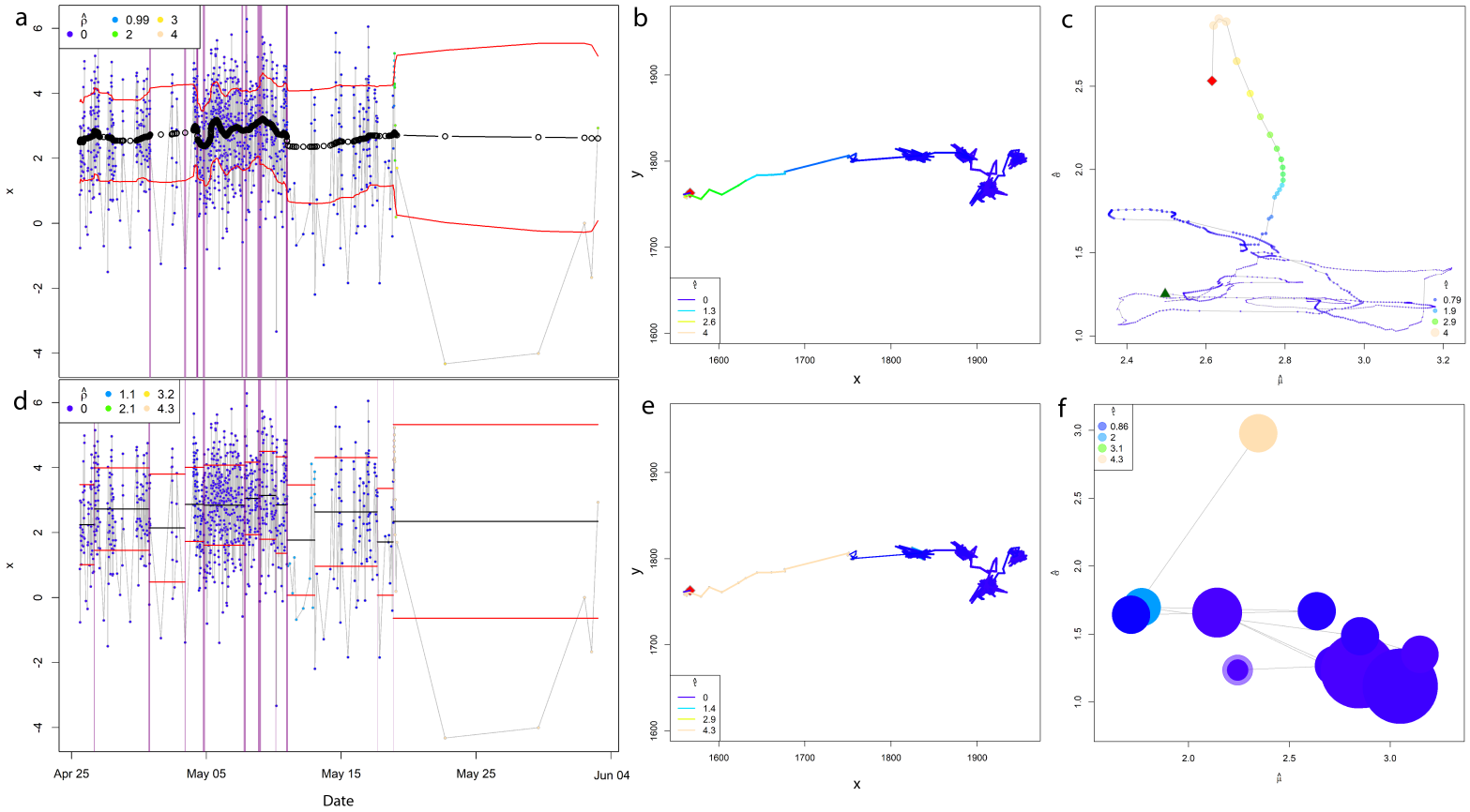

Figure A.9: BCPA analysis using the log velocity $log(V)$ of lobster 170, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 170 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 170 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

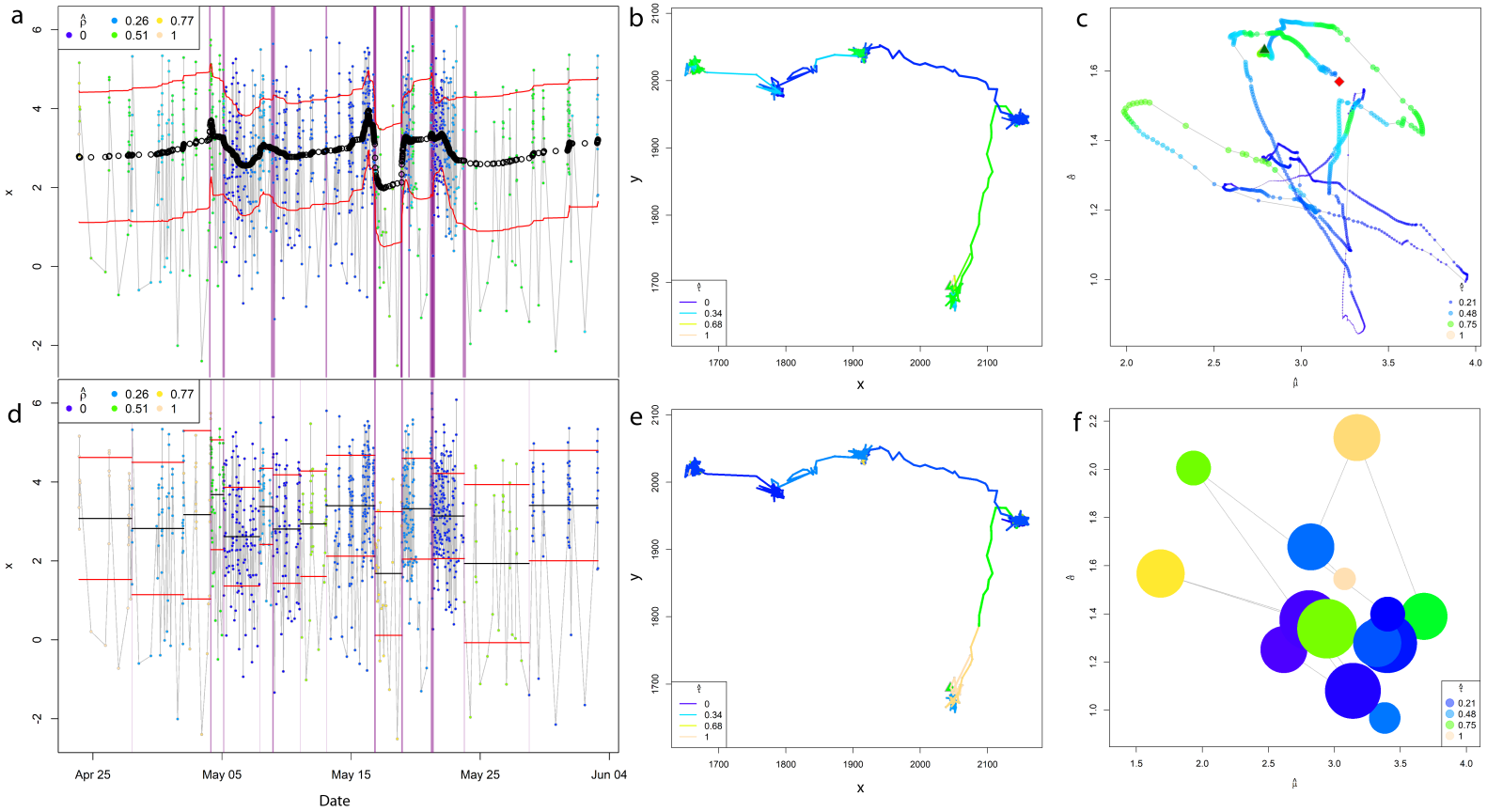

Figure A.10: BCPA analysis using the log velocity $log(V)$ of lobster 194, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 194 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 194 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

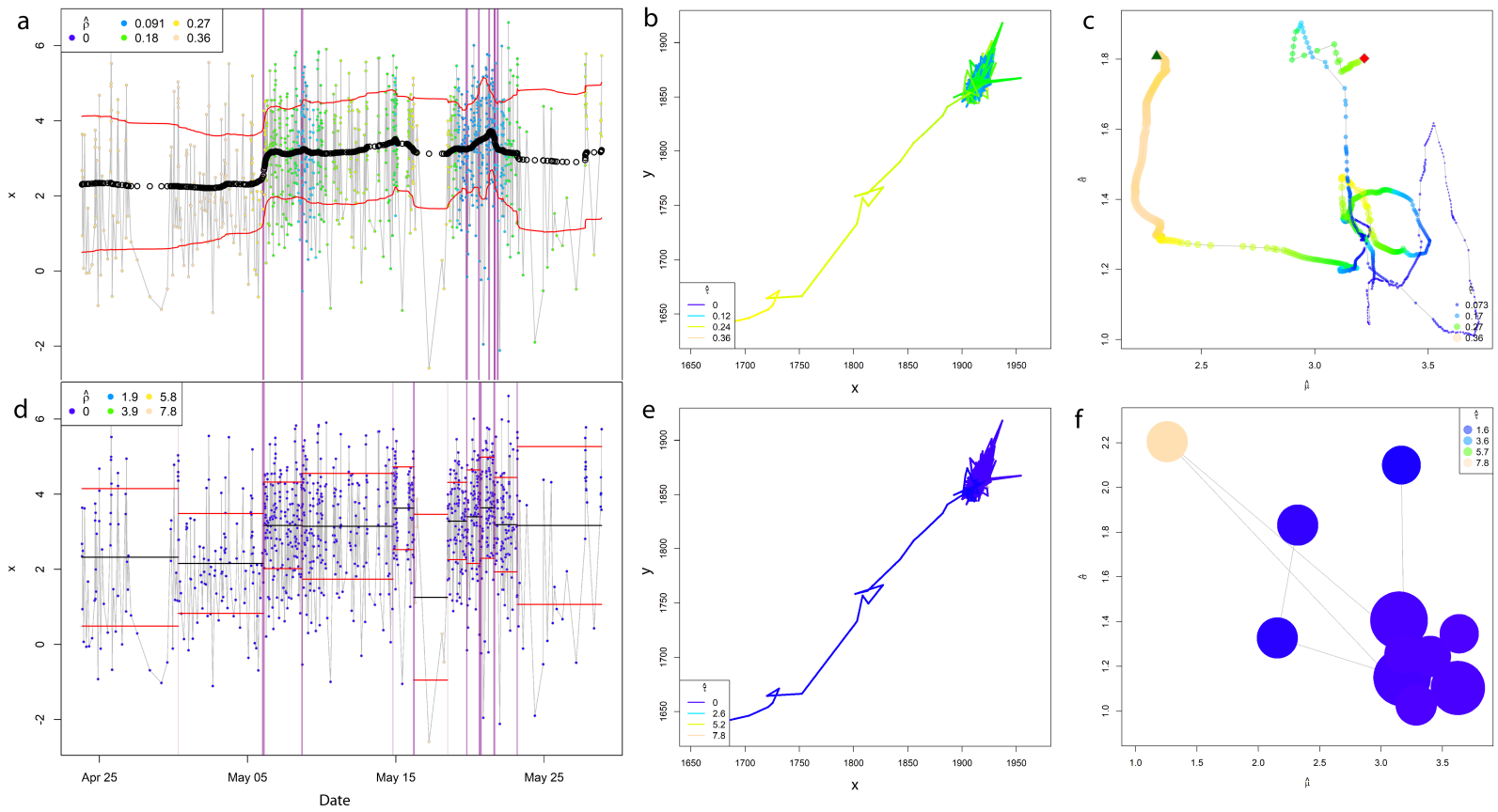

Figure A.11: BCPA analysis using the log velocity $log(V)$ of lobster 204, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 204 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 204 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

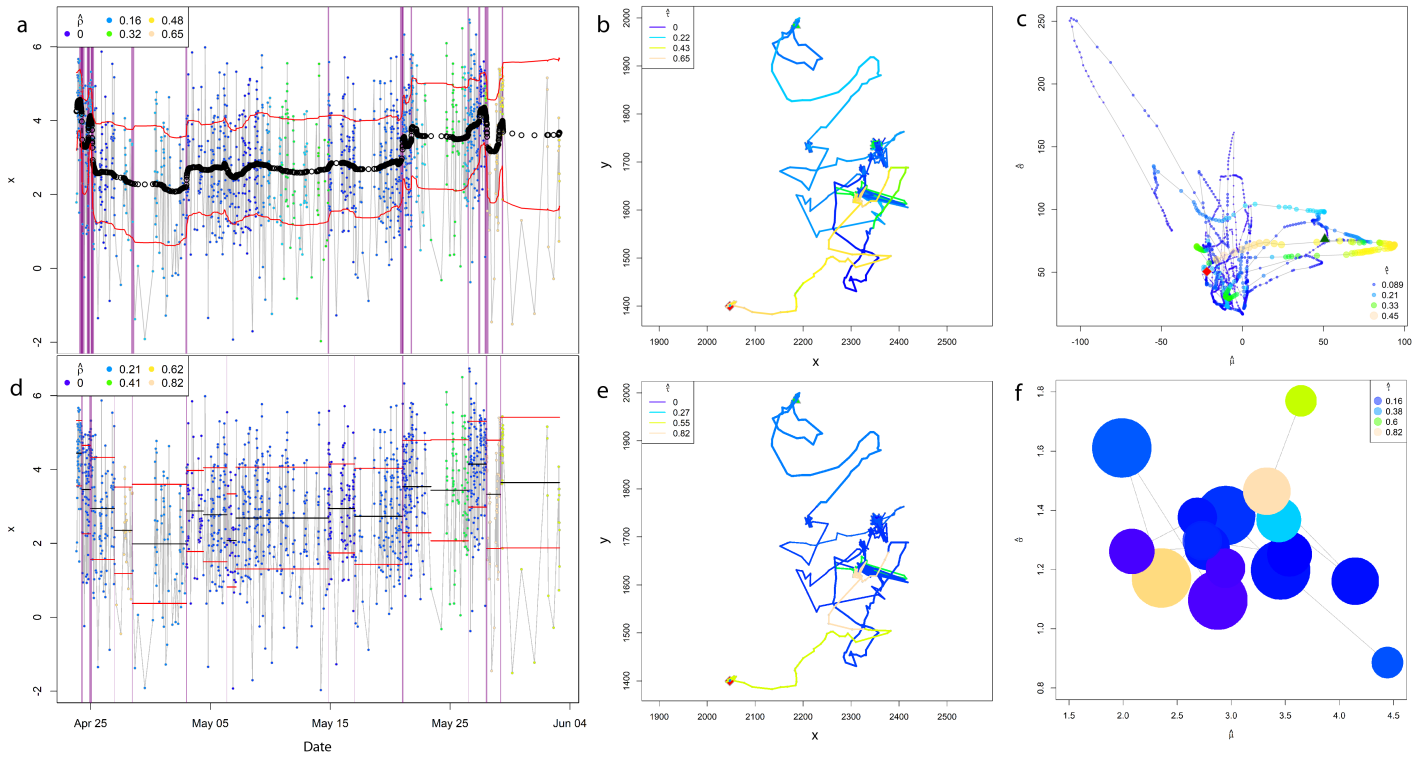

Figure A.12: BCPA analysis using the log velocity $log(V)$ of lobster 214, $K = 1.5$ a) smooth BCPA analysis, b) trajectory of lobster 214 corresponding to the smooth analysis, c) phase plot from the smooth analysis, d) flat BCPA output velocity, e) trajectory of lobster 214 corresponding to the smooth analysis, f) phase plot from the smooth analysis. Purple lines in a) and d) indicate behavioural change points, the black dots represent the mean, and the red line indicates the standard deviation. Phase plots c) and f) illustrate how the 3 parameters change in relation to each other. Other colours indicate changes in the time-scale of autocorrelation τ (see individual figure legends).

A.2 Chapter 4: Pooled estimates and variances for HMMs

Method for calculating pooled point (Equation A.1) and variance estimates (Equation A.2) (Rubin and Schenker, 1986) as detailed in McClintock (2017).

$$\overline{\theta} = \frac{1}{n}\sum_{i=1}^{n}\theta^{(i)} \tag{A.1}$$

$$var\left(\overline{\theta}\right) = \left[\frac{1}{n}\sum_{i=1}^{n} var\left(\theta^{(i)}\right)\right] + \left(1+\frac{1}{n}\right)\left[\frac{1}{n-1}\sum_{i=1}^{n}\left(\theta^{(i)}-\overline{\theta}\right)^{2}\right] \tag{A.2}$$

A.3 Chapter 4: Additional hidden Markov models tables

Table A.1: Regression coefficients for transition probabilities for models presented in Fig. 4.11 - Fig. 4.14.

Lobster	Parameter	State 1 $\rightarrow$ State 2	State 2 $\rightarrow$ State 1
159	Intercept	-2.372	-2.075
	cosinorCos (Tidal cycle, period = 12.42)	0.754	0.025
	cosinorSin (Tidal cycle, period = 12.42)	1.033	-1.099
168	Intercept	-1.821	-1.228
	cosinorCos (Hour, period = 24)	0.392	-0.140
	cosinorSin (Hour, period = 24)	-0.684	0.096
170	Intercept	-2.236	-3.234
	Hardness slope (%)	-0.010	0.016
204	Intercept	-2.368	-1.979
	cosinorCos (Tidal cycle, period = 12.42)	0.943	0.822
	cosinorSin (Tidal cycle, period = 12.42)	-0.910	1.253

Table A.2: Model estimates for best fit models that had a 1.5 h activity interval and 1 h predictive interval and that are not presented in the main text in Fig. 4.11 - Fig. 4.14. Time in states is estimated as a proportion.

			State 1		State 2	
Lobster	Model	Parameter	Estimate	CI	Estimate	CI
165	12.4 h cycle	Step mean	2.53	2.39 2.69	32.54	-48.54 113.63
		Step SD	1.92	1.77 2.08	88.43	-149.21 326.08
		Step zeromass	0.03	0.01 0.05	0.87	0.81 0.92
		Turn angle mean	0.10	-0.06 0.26	-0.004	-0.10 0.09
		Turn angle conc.	0.31	0.25 0.37	0.8	0.79 0.95
		Time in states	0.68		0.32	
194	Depth slope (°)	Step mean	3.54	3.23 3.86	26.30	-0.77 53.37
		Step SD	2.64	2.30 2.98	72.99	-6.49 152.46
		Step zeromass	0.002	-0.02 0.02	0.93	0.01 0.90
		Turn angle mean	0.58	-0.66 1.82	0.002	-0.07 0.07
		Turn angle conc.	0.07	-0.03 0.17	0.90	0.84 0.97
		Time in states	0.30		0.69	
200	12.4 h	Step mean	4.65	4.38 4.93	252.50	NA
		Step SD	3.22	3.02 3.41	822.6	NA
		Step zeromass	0.07	0.04 0.1	0.95	NA
		Turn angle mean	-3.12	-3.47 -2.77	1.58	NA
		Turn angle conc.	0.18	0.12 0.25	0.07	-0.34 0.47
		Time in states	0.56		0.44	
214	12.4 h *step*	Step mean	4.19	3.67 4.71	34.96	-6.11 76.03
		Step SD	2.87	2.37 3.38	95.58	-19.73 210.89
		Step zeromass	0.07	- 0.03 0.17	0.80	0.73 0.88
		Turn angle mean	-1.21	NA	0.32	-0.11 0.75
		Turn angle conc.	0.06	0.03 0.09	0.44	0.39 0.49
		Time in states	0.41		0.59	

References

Acheson, J. and Gardner, R. (2011). The evolution of the Maine lobster V-notch practice: Cooperation in a prisoner's dilemma game. *Ecology and Society*, **16**(1):41.

Acheson, J. M. and Brewer, J. F. (2003). Changes in the territorial system of the maine lobster industry. *The commons in the new millennium: Challenges and adaptation*, pages 37–59.

Addison, J. T. (1995). Influence of behavioural interaction on lobster distribution and abundance as inferred from pot-caught samples. *ICES Marine Science Symposium*, **199**:294–300.

Addison, J. T. and Bell, M. C. (1997). Simulation modelling of capture processes in trap fisheries for clawed lobsters. *Marine and Freshwater Research*, **48**(8):1035–1044.

Agnalt, A.-L., Kristiansen, T. S., and Jørstad, K. E. (2007). Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway. *ICES Journal of Marine Science*, **64**(2):288–297.

Allen, A. M. and Singh, N. J. (2016). Linking Movement Ecology with Wildlife Management and Conservation. *Frontiers in Ecology and Evolution*, **3**(January):1–13.

Amlaner, C. J. and Macdonald, D., editors (1980). *The evaluation of home range size and configuration using radio tracking data. A Hand- book on Biotelemetry and Radio Tracking: Proceedings of an International Conference on Telemetry and Radio Tracking in Biology and Medicine*. Pergamon Press, Oxford.

Atema, J. (1971). Sex pheromone in the lobster, *Homarus americanus*. *Nature*, **232**(5308):261–263.

Atema, J. (1986). Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**(11):2283–2290.

Atema, J. (1995). Chemical signals in the marine environment: dispersal, detection, and temporal signal analysis. *Proceedings of the National Academy of Sciences*, **92**(1):62–66.

Atema, J. and Cobb, J. S. (1980). Social behaviour. In *The Biology and. Management of Lobsters*, page 409–450. Academic Press, New York.

Atema, J., Jacobson, S., Karnofsky, E., Oleszko-Szuts, S., and Stein, L. (1979). Pair formation in the lobster, *Homarus americanus*: Behavioral development pheromones and mating. *Marine Behaviour and Physiology*, **6**(4):277–296.

Atema, J. and Voigt, R. (1995). Behavior and Sensory Biology. In Factor, J. R., editor, *Biology of the Lobster Homarus americanus*, page 313–348. Academic Press, New York.

Auger-Méthé, M., Albertsen, C., Jonsen, I., Derocher, A., Lidgard, D., Studholme, K., Bowen, W., Crossin, G., and Mills Flemming, J. (2017). Spatiotemporal modelling of marine movement data using Template Model Builder (TMB). *Marine Ecology Progress Series*, **565**:237–249.

Bahl, L., Jelinek, F., and Mercer, R. (1983). A maximum likelihood approach to continuous speech recognition. In *IEEE Transactions on Pattern Analysis and Machine Intelligence, PAMI-5*, pages 179–190.

Bailey, L. L., Simons, T. R., and Pollock, K. H. (2004). Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications*, **14**(3):692–702.

Baker, P. J. and Harris, S. (2000). Interaction rates between members of a group of Red Foxes *Vulpes vulpes*. *Mammal Review*, **30**(3-4):239–242.

Ball, B., Linnane, A., Munday, B., Browne, R., and Mercer, J. P. (2001). The effect of cover on in situ predation in early benthic phase European lobster *Homarus gammarus*. *Journal of the Marine Biological Association of the United Kingdom*, **81**:639–642.

Bannister, R. C. A. and Addison, J. T. (1986). Effect of Assumptions about the Stock–Recruitment Relationship on a Lobster (*Homarus gammarus*) Stock Assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**(11):2353–2359.

Barshaw, D. E. and Spanier, E. (1994). Anti-predator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bulletin of Marine Science*, **55**(2-3):375–382.

Beck, M. W. (1997). A test of the generality of the effects of shelter bottlenecks in four stone crab populations. *Ecology*, **78**(8):2487–2503.

Behringer, D. C., Butler, M. J., and Shields, J. D. (2006). Avoidance of disease by social lobsters. *Nature*, **441**(May):441–421.

Bell, A. M. and Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, **10**(9):828–834.

Bell, M. C. (2001). Estimating trapping areas from trap-catch data for lobsters and crabs. *Marine and Freshwater Research*, **52**:1233–42.

Benhamou, S. (2014). Of scales and stationarity in animal movements. *Ecology Letters*, **17**(3):261–272.

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., and Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, **90**:171–180.

Bennett, D. B. (1974). The effects of pot immersion time on catches of crabs, *Cancer pagurus* L. and lobsters, *Homarus gammarus* (L.). *Journal du Conseil International pour L'Exploration de la Mer*, **35**(3):332–336.

Bertness, M. D., Gaines, S. D., and Wahle, R. A. (1996). Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*, **137**(1-3):103–110.

Bertrand, M. R., DeNicola, A. J., Beissinger, S. R., and Swihart, R. K. (1996). Effects of parturition on home ranges and social affiliations of female white-tailed deer. *Journal of Wildlife Management*, **60**(4):899–909.

Beverton, R. J. H. and Holt, S. J. (1957). On the Dynamics of Exploited Fish Populations.

Beyer, H. (2012). Geospatial Modelling Environment.

Bhattacharyya, A. (1943). On a measure of divergence between two statistical populations defined by their probability distributions. *Bulletin of Calcutta Mathematical Society*, **35**:99–109.

Bjordal, A. (1986). The behaviour of Norway lobster towards baited creels and size selectivity of creels and trawl. *Fiskeridir.Skr.*, **18**(3):131–137.

Boudreau, S. and Worm, B. (2012). Ecological role of large benthic decapods in marine ecosystems: a review. *Marine Ecology Progress Series*, **469**(Cl):195–213.

Bowlby, H. D., Hanson, J. M., and Hutchings, J. A. (2007). Resident and dispersal behavior among individuals within a population of American lobster *Homarus americanus*. *Marine Ecology Progress Series*, **331**:207–218.

Bowlby, H. D., Hanson, J. M., and Hutchings, J. a. (2008). Stock structure and seasonal distribution patterns of American lobster, *Homarus americanus*, inferred through movement analyses. *Fisheries Research*, **90**:279–288.

Breithaupt, T., Lindstrom, D. P., and Atema, J. (1999). Urine release in freely moving catheterised lobsters (*Homarus americanus*) with reference to feeding and social activities. *The Journal of experimental biology*, **202**(Pt 7):837–844.

Briffa, M. and Greenaway, J. (2011). High in situ repeatability of behaviour indicates

animal personality in the beadlet anemone *Actinia equina* (Cnidaria). *PLoS ONE*, **6**(7).

Briffa, M., Rundle, S. D., and Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings. Biological sciences / The Royal Society*, **275**(1640):1305–1311.

Briones-Fourzán, P. and Lozano-Álvarez, E. (2001). Effects of artificial shelters (Casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. *Marine Ecology Progress Series*, **221**:221–232.

Broell, F., Noda, T., Wright, S., Domenici, P., Steffensen, J. F., Auclair, J. P., and Taggart, C. T. (2013). Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *Journal of Experimental Biology*, **216**(8):1522–1522.

Bushmann, P. J. and Atema, J. (1997). Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**:647–654.

Bushmann, P. J. and Atema, J. (2000). Chemically Mediated Mate Location and Evaluation in the Lobster, *Homarus americanus*. *Journal of Chemical Ecology*, **26**(4):883–899.

Butler, M. J. (2003). Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit, individual-based approach. *Fisheries Research*, **65**(1-3):63–79.

Caddy, J. and Stamatopoulos, C. (1990). Mapping growth and mortality rates of crevice-dwelling organisms onto a perforated surface: The relevance of 'cover' to the carrying capacity of natural and artificial habitats. *Estuarine, Coastal and Shelf Science*, **31**(1):87–106.

Cagnacci, F., Boitani, L., Powell, R. A., and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**(1550):2157–2162.

Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **917**:516–519.

Campbell, A. (1986). Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**:2197–2205.

Campbell, A. and Stasko, A. (1986). Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Marine Biology*, **92**(3):393–404.

Cao, J., Chen, Y., and Richards, R. A. (2017). Improving assessment of *Pandalus* stocks using a seasonal, size-structured assessment model with environmental variables. Part I: Model description and application. *Canadian Journal of Fisheries and Aquatic Sciences*, **74**(3):349–362.

Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., and Largier, J. L. (2003). Comparing Marine and Terrestrial Ecosystems : Implications for the Design of Coastal Marine Reserves. *Ecological Applications*, **13**(1 supplement):S90–S107.

Cefas (2017). Lobster (*Homarus gammarus*) Cefas Stock Status Report 2017. Technical report.

Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-, Brodersen, J., Anders Nilsson, P., Skov, C., and Brønmark, C. (2011). To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, **14**(9):871–876.

Chapman, B. B., Morrell, L. J., and Krause, J. (2010). Unpredictability in food supply during early life influences boldness in fish. *Behavioral Ecology*, **21**(3):501–506.

Chen, Y., Kanaiwa, M., and Wilson, C. (2005). Developing and evaluating a size-structured stock assessment model for the American lobster, *Homarus americanus*, fishery. *New Zealand Journal of Marine and Freshwater Research*, **39**(August 2004):645–660.

Coates, J., Hovel, K., Butler, J., Klimley, A., and Morgan, S. (2013). Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. *Marine Ecology Progress Series*, **486**:189–201.

Cobb, J. S. (1971). The shelter-related behavior of the lobster, *Homarus americanus*. *Ecology*, **52**(1):108–115.

Cobb, J. S. (1981). Behaviour of the Western Australian Spiny Lobster, *Panulirus cygnus* George, in the Field and Laboratory. *Aust.J.Mar.Freshwater Res.*, **32**(3):399–409.

Cobb, J. S. and Castro, K. M. (2006). *Homarus* species. In Phillips, B. F., editor, *Lobsters: Biology, Management, Aquaculture and Fisheries*. Blackwell Publishing, Oxford.

Collins, K. J. and Jensen, A. C. (1997). Acceptable use of waste materials. In *European Artificial Reef Research*, page 377–390. Southampton Oceanography Centre.

Colwell, R. K. and Winkler, C. W. (1984). A null model for null models in biogeography. In Strong, D. R. J., Simberloff, D., Abele, L. G., and Thistle, A. B., editors, *Ecological Communities: Conceptual Issues and the Evidence*, page 344–359. Princeton University, Princeton, NJ.

Cooper, R. and Uzmann, J. (1980). Ecology of juvenile and adult *Homarus.* In Cobb, J. S. and Phillips, B. F., editors, *The Biology and Management of Lobsters, Vol. 2*, pages 97–142. Academic Press, New York.

Cooper, R. R. A. and Uzmann, J. J. R. (1971). Migrations and Growth of Deep-Sea Lobsters, *Homarus americanus*. *Science*, **171**(3968):288–290.

Costa, D. P., Robinson, P. W., Arnould, J. P. Y., Harrison, A.-L., Simmons, S. E., Hassrick, J. L., Hoskins, A. J., Kirkman, S. P., Oosthuizen, H., Villegas-Amtmann, S., and Crocker, D. E. (2010). Accuracy of ARGOS Locations of Pinnipeds at-Sea Estimated Using Fastloc GPS. *PLoS ONE*, **5**(1):e8677.

Cote, D., Nicolas, J.-M., Whoriskey, F., Cook, A. M., Broome, J., Regular, P. M., and Baker, D. (2018). Charaterizing snow crab (*Chionoecetes opilio*) movements in the Sydney Bight (Nova Scotia, Canada): a collaborative approach using multi-scale acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*.

Cowan, D. F. and Atema, J. (1990). Moult staggering and serial monogamy in American lobsters, *Homarus americanus*. *Animal Behaviour*, pages 1199–1206.

Cowen, R. K. and Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*, **1**(1):443–466.

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., and James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, **63**(10):1495–1503.

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., Raby, G. D., and Cooke, S. J. (2017). Acoustic Telemetry and Fisheries Management. *Ecological Applications*, **27**(4):1031–1049.

Dammhahn, M. (2012). Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? *Proceedings. Biological sciences / The Royal Society*, **279**(1738):2645–51.

Davis, G. E. (1985). Artificial structures to mitigate marina construction impacts on spiny lobster *Panulirus argus*. *Bulletin of Marine Science*, **37**(1):151–156.

de Solla, S. R., Bonduriansky, R., and Brooks, R. J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, **68**(2):221–234.

Debuse, V. J., Addison, J. T., and Reynolds, J. D. (2003). Effects of breeding site density on competition and sexual selection in the European lobster. *Behavioral Ecology*, **14**(3):396–402.

Derby, C. D. and Atema, J. (1981). Selective improvement in responses to prey odors by the lobster, *Homarus americanus*, following feeding experience. *Journal of Chemical Ecology*, **7**(6):1073–1080.

Derby, C. D. and Atema, J. (1982). The function of chemo- and mechanoreceptors in

lobster (*Homarus americanus*) feeding behaviour. *Journal of Experimental Biology*, **98**(1):317–327.

Devine, D. V. and Atema, J. (1982). Function of chemoreceptor organs in spatial orientation of the lobster, *Homarus americanus*: differences and overlap. *Biological Bulletin*, **163**(1):144.

Di Lorenzo, M., D'Anna, G., Badalamenti, F., Giacalone, V., Starr, R., and Guidetti, P. (2014). Fitting the size of no-take zones to species movement patterns: a case study on a Mediterranean seabream. *Marine Ecology Progress Series*, **502**(October 2015):245–255.

Doncaster, C. P. (1990). Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology*, **143**(4):431–443.

Dow, R. (1980). The clawed lobster fisheries. In Cobb, S. and Phillips, B. F., editors, *The Biology and Management of Lobsters, Vol. 2*, page 293. Academic Press.

Dray, S., Royer-Carenzi, M., and Calenge, C. (2010). The exploratory analysis of autocorrelation in animal-movement studies. *Ecological Research*, **25**(3):673–681.

Drewe, J. A., Weber, N., Carter, S. P., Bearhop, S., Harrison, X. A., Dall, S. R. X., McDonald, R. A., and Delahay, R. J. (2012). Performance of Proximity Loggers in Recording Intra- and Inter-Species Interactions: A Laboratory and Field-Based Validation Study. *PLoS ONE*, **7**(6):e39068.

Dunnington, M. J., Wahle, R. A., Bell, M. C., and Geraldi, N. R. (2005). Evaluating local population dynamics of the American lobster, *Homarus americanus*, with trap-based mark-recapture methods and seabed mapping. *New Zealand Journal of Marine and Freshwater Research*, **39**(6):1253–1276.

Durban, J. W. and Pitman, R. L. (2012). Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? *Biology letters*, **8**(2):274–7.

Dybern, B. I. (1973). Lobster burrows in Swedish waters. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **24**:401–414.

Eckert, S. A., Moore, J. E., Dunn, D. C., van Buiten, R. S., Eckert, K. L., and Halpin, P. N. (2008). Modeling loggerhead turtle movement in the Mediterranean : importance of body size and oceanography. *Ecological Applications*, **18**(2):290–308.

Eggers, D. M., Rickard, N. A., Chapman, D. G., and Whitney, R. R. (1982). A methodology for estimating area fished for baited hooks and traps along a ground line. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**(3):448–453.

Elner, R. (1980). Lobster gear selectivity-a Canadian overview. *Canadian Technical Report of Fisheries and Aquatic Sciences*, (932):78–83.

Elvenes, S., Dolan, M. F. J., Buhl-Mortensen, P., and Bellec, V. K. (2013). An evaluation of compiled single-beam bathymetry data as a basis for regional sediment and biotope mapping. *ICES Journal of Marine Science*, **70**(4):782–792.

Ennis, G. (1978). Growth curves for Newfoundland lobsters from data on molt increment and proportion molting. Technical report, Fisheries and Environment Canada.

Ennis, G. P. (1984). Territorial behaviour of the American lobster *Homarus americanus*. *Transactions of the American Fisheries Society*, **113**:330–335.

F.A.O (2016). Global Capture Production.

Fieberg, J. (2007). Kernel density estimators of home range: Smoothing and the autocorrelation red herring. *Ecology*, **88**(4):1059–1066.

Fieberg, J. and Kochanny, C. O. (2005). Quanitfying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, **69**(4):1346.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S., and Frair, J. L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**(1550):2233–44.

Fleming, C. H., Sheldon, D., Fagan, W. F., Leimgruber, P., Mueller, T., Nandintsetseg, D., Noonan, M. J., Olson, K. A., Setyawan, E., Sianipar, A., and Calabrese, J. M. (2018). Correcting for missing and irregular data in home-range estimation. *Ecological Applications*, **28**(4):1003–1010.

Fogarty, M. (1988). Time series models of the Maine lobster fishery: the effect of temperature. *Journal of Fisheries and Aquatic Sciences*, **45**(7):1145–1153.

Fogarty, M. J. and Addison, J. T. (1997). Modelling capture processes in individual traps: entry, escapement and soak time. *ICES Journal of Marine Science*, **54**:193–205.

Franke, A., Caelli, T., and Hudson, R. J. (2004). Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models. *Ecological Modelling*, **173**(2-3):259–270.

Frusher, S. D. and Hoenig, J. M. (2003). Recent developments in estimating fishing and natural mortality and tag reporting rate of lobsters using multi-year tagging models. *Fisheries Research*, **65**(1-3):379–390.

Gabriel, P. O. and Black, J. M. (2010). Behavioural syndromes in Steller's jays: the role of time frames in the assessment of behavioural traits. *Animal Behaviour*, **80**(4):689–697.

Galparsoro, I., Borja, Á., Bald, J., Liria, P., and Chust, G. (2009). Predicting suitable

habitat for the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay), using Ecological-Niche Factor Analysis. *Ecological Modelling*, **220**(4):556–567.

Garamszegi, L. Z., Eens, M., and Török, J. (2009). Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Animal Behaviour*, **77**(4):803–812.

Gell, F. R. and Roberts, C. M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution*, **18**(9):448–455.

Gendron, L. (2005). Impact of minimum legal size increases on egg-per-recruit production, size structure, and ovigerous females in the American lobster (*Homarus americanus*) population off the Magdalen Islands (Quebec, Canada) : a case study. *New Zealand Journal of Marine and Freshwater Research*, **39**(3):661–674.

Geraldi, N. R., Wahle, R. A., and Dunnington, M. J. (2009). Habitat effects on American lobster (*Homarus americanus*) movement and density: insights from georeferenced trap arrays, seabed mapping, and tagging. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**(3):460–470.

Gherardi, F., Cenni, F., Parisi, G., and Aquiloni, L. (2010). Visual recognition of conspecifics in the American lobster, *Homarus americanus*. *Animal Behaviour*, **80**(4):713–719.

Gibson, F. A. (1967). Irish Investigation on the Lobster (*Homarus vulgaris* Edw.). *Irish Fisheries Investigations Series B*, **1**(b).

Gilg, M. R. and Hilbish, T. J. (2003). The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. *Ecology*, **84**(11):2989–2998.

Goldstein, J. S., Dubofsky, E. A., and Spanier, E. (2015). Into a rhythm: diel activity patterns and behaviour in Mediterranean slipper lobsters, *Scyllarides latus*. *ICES Journal of Marine Science*, **72 (Supple**:i147–i154.

Goñi, R., Hilborn, R., Díaz, D., Mallol, S., and Adlerstein, S. (2010). Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology Progress Series*, **400**:233–243.

González, T. M., González-Trujillo, J. D., Palmer, J. R., Pino, J., and Armenteras, D. (2017). Movement behavior of a tropical mammal: The case of *Tapirus terrestris*. *Ecological Modelling*, **360**:223–229.

Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological bulletin*, **127**(1):45–86.

Gotelli, N. J. and Graves, G. R. (1996). *Null models in ecology*. Smithsonian Institution Press, Washington, D.C.

Grabowski, J. H., Clesceri, E. J., Baukus, A. J., Gaudette, J., Weber, M., and Yund, P. O. (2010). Use of herring bait to farm lobsters in the Gulf of Maine. *PLoS ONE*, **5**(4):e10188.

Grimm, V. (1999). Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling*, **115**(2-3):129–148.

Grimm, V. and Berger, U. (2016). Structural realism, emergence, and predictions in next-generation ecological modelling: Synthesis from a special issue. *Ecological Modelling*, **326**:177–187.

Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M., and Botsford, L. W. (2011a). Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation*, **144**(2):692–702.

Grüss, A., Kaplan, D. M., and Hart, D. R. (2011b). Relative impacts of adult movement, larval dispersal and harvester movement on the effectiveness of reserve networks. *PLoS ONE*, **6**(5):e19960.

Gundersen, K. (1962). Tagging experiments on lobster (*Homarus vulgaris* L.) in Norway. *Annals of Biology*, **19**(189).

Gurarie, E., Andrews, R. D., and Laidre, K. L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**(5):395–408.

Gurarie, E., Bracis, C., Delgado, M., Meckley, T. D., Kojola, I., and Wagner, C. M. (2016). What is the animal doing? Tools for exploring behavioural structure in animal movements. *Journal of Animal Ecology*, **85**(1):69–84.

Gutzler, B. and Butler IV, M. J. (2015). Casitas: a location-dependent ecological trap for juvenile Carribean spiny lobsters, *Panulirus argus*. *ICES Journal of Marine Science*, **72(Supplem**(June):i177–i184.

Haarr, M. L., Sainte-Marie, B., Comeau, M., Tremblay, M. J., and Rochette, R. (2018). Female American lobster (*Homarus americanus*) size-at-maturity declined in Canada during the 20th and early 21st centuries. *Canadian Journal of Fisheries and Aquatic Sciences*, **75**(6):908–924.

Hagen, N. T. and Mann, K. (1992). Functional response of the predators American lobster *Homarus americanus* (Milne-Edwards) and Atlantic wolffish *Anarhichas lupus* (L.) to increasing numbers of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *Journal of Experimental Marine Biology and Ecology*, **159**(1):89–112.

Hallbäck, H. and Waren, A. (1972). Food ecology of lobster, *Homarus vulgaris* in Swedish waters.

Hanson, J. M. (2009). Predator prey interactions of American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence, Canada. *New Zealand Journal of Marine and Freshwater Research*, **43**(1):69–88.

Hedgecock, D., Nelson, K., Simons, J., and Shleser, R. (1977). Genic similarity of American and European species of the lobster *Homarus*. *The Biological Bulletin*, **152**:41–50.

Hemson, G., Johnson, P. J., South, A., Kenward, R., Ripley, R., and Macdonald, D. (2005). Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology*, **74**(3):455–463.

Herrnkind, W. F. (1983). Movement patterns and orientation. In Vernberg, F. J. and Wernberg, W. B., editors, *The biology of crustacea Vol.7*, pages 41–105. Academic Press, New York.

Heupel, M. R., Semmens, J. M., and Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, **57**(1):1.

Hilborn, R. (1997). Lobster stock assessment: report from a workshop; II. *Marine and Freshwater Research*, **48**(8):945.

Hilborn, R. and Walters, C. J. (1992). *Quantitative fisheries stock assessment: choice, dynamics, and uncertainty*. Chapman and Hall, London.

Hixon, M. A. and Beets, J. P. (1989). Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, **44**(2):666–680.

Hobday, A. J., Hartog, J. R., Spillman, C. M., and Alves, O. (2011). Seasonal forecasting of tuna habitat for dynamic spatial management. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**(5):898–911.

Hockersmith, E. and Beeman, J. (2012). A History of Telemetry in Fishery Research. In Adams, N., Beeman, J. W., and Eiler, J. H., editors, *Telemetry techniques: a user guide for fisheries research*, pages 7–20. American Fisheries Society, Bethesda, Maryland, USA.

Højsgaard, S., Halekoh, U., and Yan, J. (2006). The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software*, **15**(2):1–11.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences*, **105**(49):19060–19065.

Hooker, S., Cañadas, A., Hyrenbach, K., Corrigan, C., Polovina, J., and Reeves, R. (2011). Making protected area networks effective for marine top predators. *Endangered Species Research*, **13**(3):203–218.

Horner, A. J. (2004). Dual antennular chemosensory pathways can mediate orientation by Caribbean spiny lobsters in naturalistic flow conditions. *Journal of Experimental Biology*, **207**(21):3785–3796.

Horton, G. E. and Letcher, B. H. (2008). Movement patterns and study area boundaries: influences on survival estimation in capture mark recapture studies. *Oikos*, **117**(March):1131–1142.

Hovel, K. A. and Wahle, R. A. (2010). Effects of habitat patchiness on American lobster movement across a gradient of predation risk and shelter competition. *Ecology*, **91**(7):1993–2002.

Howard, A. E. (1980). Substrate controls on the size composition of lobster (*Homarus gammarus*) populations. *Journal du Conseil International pour L'Exploration de la Mer*, **39**(2):130–133.

Howard, A. E. and Nunny, R. S. (1983). Effects of near-bed current speeds on the distribution and behaviour of the lobster *Homarus gammarus* (L.). *Journal of Experimental Marine Biology and Ecology*, **71**:27–42.

Howarth, L. M., Dubois, P., Gratton, P., Judge, M., Christie, B., Waggitt, J. J., Hawkins, J. P., Roberts, C. M., and Stewart, B. D. (2016). Trade-offs in marine protection: multispecies interactions within a community-led temperate marine reserve. *ICES Journal of Marine Science: Journal du Conseil*, **74**(1):fsw166.

Hudon, C. (1994). Large-scale analysis of Atlantic Nova Scotia American Lobster (*Homararus americanus*) landings with respect to habitat, temperature, and wind conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**:1308–1321.

Hughes, J. P., Guttorp, P., and Charles, S. P. (1999). A non-homogeneous hidden Markov model for precipitation occurrence. *Journal of the Royal Statistical Society. Series C (Applied Statistics)*, **48**(1):15–30.

Huntingford, F. A. (1982). Do inter- and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Animal Behaviour*, **30**(3):909–916.

Hurford, A. (2009). GPS measurement error gives rise to spurious 180° turning angles and strong directional biases in animal movement data. *PLoS ONE*, **4**(5).

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Mills Flemming, J. E., and Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, **348**(6240):1255642–1255642.

Hutchings, J. A., Bishop, T. D., and McGregor-Shaw, C. R. (1999). Spawning behaviour of Atlantic cod, *Gadus morhua*: evidence of mate competition and mate choice in a broadscale spawner. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**(1):97–104.

Incze, L. and Wahle, R. A. (1991). Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus*. *Marine Ecology Progress Series*, **79**(1-2):77–87.

Jensen, A. (2002). Artificial reefs of Europe: perspective and future. *ICES Journal of Marine Science*, **59**:S3–S13.

Jensen, A. C., Collins, K. J., Free, E. K., and Bannister, R. C. A. (1994). Lobster (*Homarus gammarus*) movement on an artificial reef: the potential use of artificial reefs for stock enhancement. *Crustaceana*, **67**(2):198–211.

Jernakoff, P. and Phillips, B. F. (1988). Effect of a baited trap on the foraging movements of juvenile western rock lobsters, *Panulirus cygnus* George. *Australian Journal of Marine & Freshwater Research*, **39**(2):185–192.

Johnson, D. H. (1999). The Insignificance of Statistical Significance Testing. *The Journal of Wildlife Management*, **63**(3):763–772.

Johnson, D. S., London, J. M., Lea, M.-A., and Durban, J. W. (2008). Continuous-Time Correlated Random Walk Model for Animal Telemetry Data. *Ecology*, **89**(5):1208–1215.

Jones, R. (1981). The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis). *FAO Fisheries Circulars*, **734**.

Jones, R. (1984). Assessing the effects of composition data in fish stock assessment (with notes on VPA and cohort analysis. Technical report, FAO, Rome.

Jonsen, I., Basson, M., Bestley, S., Bravington, M., Patterson, T., Pedersen, M., Thomson, R., Thygesen, U., and Wotherspoon, S. (2013). State-space models for bio-loggers: A methodological road map. *Deep Sea Research Part II: Topical Studies in Oceanography*, **88-89**:34–46.

Jonsen, I. D. (2016). Joint estimation over multiple individuals improves behavioural state inference from animal movement data. *Scientific Reports*, **6**(1):20625.

Jonsen, I. D., Flemming, J. M., and Myers, R. A. (2005). Robust state–space modeling of animal movement data. *Ecology*, **86**(11):2874–2880.

Jury, S., Howell, H., O'Grady, D. F., and Watson III, W. H. (2001). Lobster trap video: in situ video surveillance of the behaviour of *Homarus americanus* in and around traps. *Marine & Freshwater Research*, **52**:1125–32.

Jury, S. H., Langley, T., Gutzler, B. C., Goldstein, J. S., and Watson, W. H. (2018).

Monitoring the behavior of freely moving lobsters with accelerometers. *Bulletin of Marine Science*, **94**(3):533–553.

Jury, S. H. and Watson, W. H. I. (2013). Seasonal and Sexual differences in the thermal prefrences and movement of American lobsters. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**(July):1650–1657.

Kafas, A., McLay, A., Chimienti, M., Scott, B. E., Davies, I., and Gubbins, M. (2017). ScotMap: Participatory mapping of inshore fishing activity to inform marine spatial planning in Scotland. *Marine Policy*, **79**(February):8–18.

Kaplan, L. J., Lowrance, C., Basil, J., and Atema, J. (1993). The role of chemical and visual cues in agonistic interactions of the American lobster. *Biological Bulletin*, **185**(3):320–321.

Karavanich, C. and Atema, J. (1993). Agonistic encounters in the American lobster, *Homarus americanus*: do they remember their opponents? *Biological Bulletin*, **185**(October):321–322.

Karavanich, C. and Atema, J. (1998a). Individual recognition and memory in lobster dominance. *Animal Behaviour*, **56**(6):1553–1560.

Karavanich, C. and Atema, J. (1998b). Olfactory recognition of urine signals in dominance fights between male lobster, *Homarus americanus*. *Behaviour*, **135**(6):719–730.

Karnofsky, E. B., Atema, J., and Elgin, R. H. (1989a). Field Observations of Social Behavior, Shelter Use, and Foraging in the Lobster, *Homarus americanus*. *Biological Bulletin*, **176**(3):239–246.

Karnofsky, E. B., Atema, J., and Elgin, R. H. (1989b). Natural dynamics of population structure and habitat use of the lobster *Homarus americanus*, in a shallow cove. *Biological Bulletin*, **176**(1972):247–256.

Karnofsky, E. B. and Price, H. J. (1989a). Behavioural response of the lobster *Homarus americanus* to traps. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**:1625–1632.

Karnofsky, E. B. and Price, H. J. (1989b). Dominance, territoriality and mating in the lobster, *Homarus americanus*: A mesocosm study. *Marine Behaviour and Physiology*, **15**(2):101–121.

Kelly, S., Scott, D., MacDiarmid, A., and Babcock, R. C. (2000). Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation*, **92**(3):359–369.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. a., Cagnacci, F., Mitchell, M. S., Gaillard, J.-M., and Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical*

transactions of the Royal Society of London. Series B, Biological sciences, **365**(1550):2221–31.

Kjær, L. J., Schauber, E. M., and Nielsen, C. K. (2008). Spatial and Temporal Analysis of Contact Rates in Female White-Tailed Deer. *Journal of Wildlife Management*, **72**(8):1819–1825.

Krouse, J. (1989). Performance and selectivity of trap fisheries for crustaceans. In Caddy, J., editor, *Marine Invertebrate Fisheries: Their Assessment and Management*, pages 307–325. John Wiley & Sons., New York.

Langhamer, O., Wilhelmsson, D., and Engström, J. (2009). Artificial reef effect and fouling impacts on offshore wave power foundations and buoys – a pilot study. *Estuarine, Coastal and Shelf Science*, **82**(3):426–432.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., and Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. *Ecology*, **93**(11):2336–2342.

Laurel, B., Gregory, R., Brown, J., Hancock, J., and Schneider, D. (2004). Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and G. ogac: the role of movement and aggregation. *Marine Ecology Progress Series*, **272**:257–270.

Lawton, P. and Lavalli, K. (1995). Postlarval, juvenile, adolescent and adult ecology. In Factor, J. R., editor, *Biology of the Lobster, Homarus Americanus*, page 120–122. Academic Press, Inc.

Leimar, O. and Enquist, M. (1984). Effects of asymmetries in owner-intruder conflicts. *Journal of Theoretical Biology*, **111**(3):475–491.

LeMunyan, C. D., White, W., Nyberg, E., and Christian, J. J. (1959). Design of a miniature radio transmitter for use in animal studies. *The Journal of Wildlife Management*, **23**(1):107–110.

Leos-Barajas, V., Gangloff, E. J., Adam, T., Langrock, R., van Beest, F. M., Nabe-Nielsen, J., and Morales, J. M. (2017a). Multi-scale Modeling of Animal Movement and General Behavior Data Using Hidden Markov Models with Hierarchical Structures. *Journal of Agricultural, Biological, and Environmental Statistics*, **22**(3):232–248.

Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y. Y., Murgatroyd, M., and Papastamatiou, Y. P. (2017b). Analysis of animal accelerometer data using hidden Markov models. *Methods in Ecology and Evolution*, **8**(2):161–173.

Linnane, A., Ball, B., Mercer, J. P., Browne, R., Meeren, G. V. D., Ringvold, H., Bannister, C., Mazzoni, D., and Munday, B. (2001). Searching for the early benthic

phase (EBP) of the European lobster: A trans-European study of cobble fauna. *Hydrobiologia*, **465**:63–72.

Linnane, A., Mazzoni, D., and Mercer, J. P. (2000). A long-term mesocosm study on the settlement and survival of juvenile European lobster Homarus gammarus L. in four natural substrata. *Journal of Experimental Marine Biology and Ecology*, **249**(1):51–64.

Lizárraga-Cubedo, H., Tuck, I., Bailey, N., Pierce, G., and Kinnear, J. (2003). Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus*. *Fisheries Research*, **65**(1-3):137–152.

Long, J. A. and Nelson, T. A. (2013). Measuring dynamic interaction in movement data. *Transactions in GIS*, **17**(1):62–77.

Long, J. A., Nelson, T. A., Webb, S. L., and Gee, K. L. (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology*, pages 1216–1233.

Lovewell, S. R. J., Howard, A. E., and Bennett, D. B. (1988). The effectiveness of parlour pots for catching lobsters (*Homarus gammarus (L.)*) and crabs (*Cancer pagurus L.*). *Journal du Conseil International pour L'Exploration de la Mer*, **44**:247–252.

Lyons, G. N., Halsey, L. G., Pope, E. C., Eddington, J. D., and Houghton, J. D. (2013). Energy expenditure during activity in the American lobster *Homarus americanus*: Correlations with body acceleration. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **166**(2):278–284.

Mackie, A. M., Grant, P. T., Shelton, R. G. J., Hepper, B. T., and Walne, P. R. (1980). The relative efficiencies of natural and artificial baits for the lobster, *Homarus gammarus* laboratory and field trials [Bay of Nigg, Aberdeen, Scotland]. *Journal du Conseil International pour L'Exploration de la Mer*, **39**(2):123–129.

Marine Management Organisation (2017). UK sea fisheries annual statistics report 2016. Technical report, Marine Management Organisation.

Mather, J. A. and Anderson, R. C. (1993). Personalities of octopuses (*Octopus rubescens*). *Journal of Comparitive Psychology*, **107**(3):336–340.

Mathies, N. N. H., Ogburn, M. M. B., McFall, G., and Fangman, S. (2014). Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Marine Ecology Progress Series*, **495**:27–38.

Maunder, M. N. and Punt, A. E. (2004). Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, **70**(2-3):141–159.

Maunder, M. N., Sibert, J. R., Fonteneau, A., Hampton, J., Kleiber, P., and Harley, S. J. (2006). Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science*, **63**(8):1373–1385.

Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., Fossette, S., Hobday, A. J., Bennett, M., Benson, S., Caldwell, M. R., Costa, D. P., Dewar, H., Eguchi, T., Hazen, L., Kohin, S., Sippel, T., and Crowder, L. B. (2015). Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, **58**(May):42–50.

McClintock, B. T. (2017). Incorporating Telemetry Error into Hidden Markov Models of Animal Movement Using Multiple Imputation. *Journal of Agricultural, Biological and Environmental Statistics*, **22**(3):249–269.

McClintock, B. T. and Michelot, T. (2017). momentuHMM : R package for analysis of telemetry data using generalized multivariate hidden Markov models of animal movement.

McKellar, A. E., Langrock, R., Walters, J. R., and Kesler, D. C. (2015). Using mixed hidden Markov models to examine behavioral states in a cooperatively breeding bird. *Behavioral Ecology*, **26**(1):148–157.

McLeese, D. and Wilder, D. (1958). The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *Journal of the Fisheries Board of Canada*, pages 1345–1354.

McMahan, M. D., Brady, D. C., Cowan, D. F., Grabowski, J. H., and Sherwood, G. D. (2013). Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **70**(11):1625–1634.

McQuinn, I. H., Gendron, L., and Himmelman, J. H. (1988). Area of attraction and effective area fished by a welk (*Buccinum undatum*) trap under variable conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**(12):2054–2060.

Meeren, G. I. v. d. (1997). Preliminary acoustic tracking of native and transplanted European lobsters (*Homarus gammarus*) in an open sea lagoon. *Marine and Freshwater Research*, **48**(8):915.

Mehrtens, F., Stolpmann, M., Buchholz, F., Hagen, W., and Saborowski, R. (2005). Locomotory activity and exploration behaviour of juvenile European lobsters (*Homarus gammarus*) in the laboratory. *Marine and Freshwater Behaviour and Physiology*, **38**(2):105–116.

Mercer, J. P., Bannister, R. C. A., Van der Meeren, G. I., Debuse, V. J., Mazzoni, D., Lovewell, S., Browne, R., Linnane, A., and Ball, B. (2001). An overview of the LEAR (Lobster Ecology and Recruitment) project: Results of field and experimental studies on the juvenile ecology of *Homarus gammarus* in cobble. *Marine and Freshwater Research*, **52**(8):1291–1301.

Mesquita, C., Meithe, T., Dobby, H., and McLay, A. (2017). Crab and lobster fisheries in Scotland: results of stock assessments 2013-2015. Technical Report 14, Marine Scotland.

Michelena, P., Jeanson, R., Deneubourg, J. L., and Sibbald, A. M. (2010). Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **277**(1684):1093–1099.

Michelot, T., Blackwell, P. G., and Matthiopoulos, J. (2018). Linking resource selection and step selection models for habitat preferences in animals. *Ecology*.

Michelot, T., Langrock, R., Bestley, S., Jonsen, I. D., Photopoulou, T., and Patterson, T. A. (2017). Estimation and simulation of foraging trips in land-based marine predators. *Ecology*, **98**(7):1932–1944.

Michelot, T., Langrock, R., and Patterson, T. (2016a). moveHMM An R package for the analysis of animal movement data.

Michelot, T., Langrock, R., and Patterson, T. A. (2016b). moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, **7**(11):1308–1315.

Miller, J. A. (2015). Towards a Better Understanding of Dynamic Interaction Metrics for Wildlife: a Null Model Approach. *Transactions in GIS*, **19**(3):342–361.

Miller, R. (1990). Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**(6):1228–1251.

Miller, R. J. (1976). Saturation of crab traps : reduced entry and escapement. *Journal du Conseil International pour L'Exploration de la Mer*, **38**(3):338–345.

Miller, R. J. (1980). Design criteria for crab traps. *ICES Journal of Marine Science*, **39**(2):140–147.

Miller, R. J. (1989). Catchability of American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* by traps. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**:1652–1657.

Miller, R. J. (1995). Catchability coefficients for American lobster (Homarus americanus). *ICES Marine Science Symposia*, **199**:349–356.

Miller, R. J. and Addison, J. T. (1995). Trapping interactions of crabs and American lobster in laboratory tanks. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**(2):315–324.

Miller, R. J. and Rodger, R. (1996). Soak times and fishing strategy for American Lobster. *Fisheries Research*, **26**:199–205.

Miller, R. J., Sharp, G. J., and O'Brien, E. M. (2006). Laboratory experiments on artificial reefs for American lobsters. *Journal of Crustacean Biology*, **26**(4):621–627.

Millspaugh, J. J., Gitzen, R. A., Kernohan, B. J., Larson, M. A., and Clay, C. L. (2004). Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin*, **32**(1):148–157.

Millspaugh, J. J., Nielson, R. M., Mcdonald, L., John, M., Gitzen, R. A., Rittenhouse, C. D., Hubbard, M. W., and Sheriff, S. L. (2006). Analysis of Resource Selection Using Utilization Distributions. *Journal of Wildlife Management*, **70**(2):384–395.

Mingozzi, T., Mencacci, R., Cerritelli, G., Giunchi, D., and Luschi, P. (2016). Living between widely separated areas: Long-term monitoring of Mediterranean loggerhead turtles sheds light on cryptic aspects of females spatial ecology. *Journal of Experimental Marine Biology and Ecology*, **485**:8–17.

Mohr, C. O. (1947). Table of Equivalent Populations of North American Small Mammals. *The American Midland Naturalist*, **37**(1):223–249.

Moland, E., Moland Olsen, E., Knutsen, H., Knutsen, J., Enersen, S., André, C., and Stenseth, N. (2011a). Activity patterns of wild European lobster *Homarus gammarus* in coastal marine reserves: implications for future reserve design. *Marine Ecology Progress Series*, **429**:197–207.

Moland, E., Olsen, E. M., Andvord, K., Knutsen, J. A., Stenseth, N. C., and Sainte-Marie, B. (2011b). Home range of European lobster (*Homarus gammarus*) in a marine reserve: implications for future reserve design. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**(7):1197–1210.

Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., André, C., and Knutsen, J. A. (2013). Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before-after control-impact study. *Proceedings. Biological sciences / The Royal Society*, **280**(1754):20122679.

Molfese, C., Beare, D., and Hall-Spencer, J. M. (2014). Overfishing and the Replacement of Demersal Finfish by Shellfish: An Example from the English Channel. *PLoS ONE*, **9**(7):e101506.

Monnahan, C. C., Ono, K., Anderson, S. C., Rudd, M. B., Hicks, A. C., Hurtado-Ferro, F., Johnson, K. F., Kuriyama, P. T., Licandeo, R. R., Stawitz, C. C., Taylor, I. G., and Valero, J. L. (2016). The effect of length bin width on growth estimation in integrated age-structured stock assessments. *Fisheries Research*, **180**:103–112.

Moore, P. and Atema, J. (1988). A model of a temporal filter in chemoreception to

extract directional information from a turbulent odor plume. *The Biological Bulletin*, **174**(3):355–363.

Moore, P. and Howarth, J. (1996). Foraging by marine scavengers: Effects of relatedness, bait damage and hunger. *Journal of Sea Research*, **36**(3-4):267–273.

Moore, P. A., Scholz, N., and Atema, J. (1991). Chemical orientation of lobsters, *Homarus americanus*, in turbulent odor plumes. *Journal of Chemical Ecology*, **17**(7):1293–1307.

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., and Fryxell, J. M. (2004). Extracting More Out of Relocation Data: Building Movement Models As Mixtures of Random Walks. *Ecology*, **85**(9):2436–2445.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H., and Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society of London*, **365**(1550):2289–2301.

Mowles, S. L., Cotton, P. A., and Briffa, M. (2012). Consistent crustaceans: the identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology*, **66**(7):11087–1094.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, **105**(49):19052–19059.

NIFCA (2017). Lobster V-notching report. Technical report.

O'Grady, D. F., Jury, S. H., and Watson, W. H. I. (2001). Use a treadmill to study the relationship between walking, ventilation and heart rate in the lobster *Homarus gammarus*. *Marine And Freshwater Research*, **52**:1387–1394.

Oppenheim, N. G. and Wahle, R. A. (2013). Cannibals by night? In situ video monitoring reveals diel shifts in inter- and intra-specific predation on the American lobster. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**(11):1635–1640.

Øresland, V., Ulmestrand, M., Agnalt, A.-L., and Oxby, G. (2017). Recorded captures of American lobster *Homarus americanus* in Swedish waters and an observation of predation on the European lobster, *Homarus gammarus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **74**(10):1503–1506.

Orians, G. and Pearson, N. (1979). On the theory of central place foraging. In Horn, D. J., Stairs, G. R., and Mitchell, R. D., editors, *Analysis of Ecological Systems*, page 155–177. Ohio State University Press, Ohio.

Page, J. L., Dickman, B. D., Webster, D. R., and Weissburg, M. J. (2011). Getting ahead:

context-dependent responses to odorant filaments drive along-stream progress during odor tracking in blue crabs. *Journal of Experimental Biology*, **214**(9):1498–1512.

Patterson, T. A., Basson, M., Bravington, M. V., and Gunn, J. S. (2009). Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology*, **78**(6):1113–1123.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., and Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution*, **23**(2):87–94.

Pawson, M. G. (1995). Biogeographical identification of English channel fish and shellfish stocks. *Fisheries research technical*, **99**(99):72.

Pechenik, J. (1999). On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, **177**:269–297.

Pedersen, M. W., Righton, D., Thygesen, U. H., Andersen, K. H., and Madsen, H. (2008). Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**(Nielsen 2004):2367–2377.

Pezzack, D. and Duggan, D. (1986). Evidence of Migration and Homing of Lobster (*Homarus americanus*) on the Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**(11):2206–2211.

Pinheiro, J. C., Bates, D. M., DebRoy, S., and Sarkar, D. (2015). nlme: linear and nonlinear mixed effects models. R package version 3.1–120.

Pittman, S. J. and McAlpine, C. A. (2003). *Movements of marine fish and decapod crustaceans: Process, theory and application*, volume 44, page 207. Academic Press.

Pohle, J., Langrock, R., van Beest, F., and Schmidt, N. M. (2017). Selecting the Number of States in Hidden Markov Models - Pitfalls, Practical Challenges and Pragmatic Solutions. *Journal of Agricultural, Biological, and Environmental Statistics*, **22**(3):270–293.

Poole, K. G. (1995). Spatial organization of a lynx population. *Canadian Journal of Zoology*, **73**(4):632–641.

Pottle, R. A. and Elner, R. W. (1982). Substrate preference behavior of juvenile american lobsters, *Homarus americanus*, in gravel and silt-clay sediments. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**(56585):928–932.

Prentice, R. L., Williams, B. J., and Peterson, A. V. (1981). On the regression analysis of multivariate failure time data. *Biometrika*, **68**(2):373–379.

Punt, A. E., Haddon, M., and McGarvey, R. (2016). Estimating growth within

size-structured fishery stock assessments: What is the state of the art and what does the future look like? *Fisheries Research*, **180**:147–160.

Punt, A. E., Huang, T., and Maunder, M. N. (2013). Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. *ICES Journal of Marine Science*, **70**(1):16–33.

Quinn II, T. J. and Deriso, R. B. (1999). *Quantitative Fish Dynamics*. Oxford University Press, New York.

R Core Team (2017). R: A Language and Environment for Statistical Computing.

Réale, D., Martin, J., Coltman, D. W., Poissant, J., and Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, **22**(8):1599–1607.

Reidenbach, M. A. and Koehl, M. A. R. (2011). The spatial and temporal patterns of odors sampled by lobsters and crabs in a turbulent plume. *Journal of Experimental Biology*, **214**(18):3138–3153.

Remelgado, R., Leutner, B., Safi, K., Sonnenschein, R., Kuebert, C., and Wegmann, M. (2017). Linking animal movement and remote sensing - mapping resource suitability from a remote sensing perspective. *Remote Sensing in Ecology and Conservation*, pages 1–14.

Reynolds, B. F., Powers, S. P., and Bishop, M. A. (2010). Application of acoustic telemetry to assess residency and movements of rockfish and lingcod at created and natural habitats in Prince William sound. *PLoS ONE*, **5**(8):2–9.

Richards, A. and Cobb, J. S. (1983). Effects of behavioral interactions on the catchability of American lobster, *Homarus americanus*, and two species of cancer crab. *Fishery Bulletin*, **81**(1):51–60.

Ricker, W. E. (1975). *Computation and Interpretation of Biological Statistics of Fish Populations*. Department of the Environment Fisheries and Marine Service.

Roach, M., Cohen, M., Forster, R., Revill, A. S., and Johnson, M. (2018). The effects of temporary exclusion of activity due to wind farm construction on a lobster (*Homarus gammarus*) fishery suggests a potential management approach. *ICES Journal of Marine Science*, **75**(February):1416–1426.

Robertson, L. M., Wang, G., McGaw, I. J., and Wringe, B. F. (2016). The effect of temperature on foraging activity and digestion in the American lobster *Homarus americanus* (Milne Edwards, 1837) (Decapoda: Nephropsidae) feeding on blue mussels *Mytilus edulis* (Linnaeus, 1758). *Journal of Crustacean Biology*, **36**(2):138–146.

Robinson, C. A., Thom, T. J., and Lucas, M. C. (2000). Ranging behaviour of a large

freshwater invertebrate, the white-clawed crayfish *Austropotamobius pallipes*. *Freshwater Biology*, **44**(3):509–521.

Rooney, S. M., Wolfe, A., and Hayden, T. J. (1998). Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review*, **28**(2):89–98.

Rowe, S. (2002). Population parameters of American lobster inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Fisheries Research*, **56**:167–175.

Ru, X., Zhang, L., Liu, S., and Yang, H. (2017). Reproduction affects locomotor behaviour and muscle physiology in the sea cucumber, *Apostichopus japonicus*. *Animal Behaviour*, **133**:223–228.

Rubin, D. B. and Schenker, N. (1986). Multiple imputation for interval estimation from simple random samples with ignorable nonresponse. *Journal of the American Statistical Association*, **81**(394):366–374.

Rudin, F. S. and Briffa, M. (2012). Is boldness a resource-holding potential trait? Fighting prowess and changes in startle response in the sea anemone, *Actinia equina*. *Proceedings of the Royal Society B: Biological Sciences*, **279**(1735):1904–1910.

Rydén, T., Teräsvirta, T., and Åsbrink, S. (1998). Stylized facts of daily return series and the hidden Markov model. *Journal of Applied Econometrics*, **13**(3):217–244.

Sainte-Marie, B., Hoskin, M. G., Coleman, R. A., von Carlshausen, E., and Davis, C. M. (2011). Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**(2):185–200.

Sale, P., Cowen, R., Danilowicz, B., Jones, G., Kritzer, J., Lindeman, K., Planes, S., Polunin, N. V. C., Russ, G., and Sadovy, Y. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution*, **20**(2):74–80.

Scales, K. L., Hazen, E. L., Jacox, M. G., Edwards, C. A., Boustany, A. M., Oliver, M. J., and Bograd, S. J. (2017). Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. *Ecography*, **40**(1):210–220.

Scales, K. L., Miller, P. I., Hawkes, L. a., Ingram, S. N., Sims, D. W., and Votier, S. C. (2014). On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, pages n/a–n/a.

Scarratt, D. J. (1968). An artificial reef for lobsters (*Homarus americanus*). *Fisheries Research Board of Canada*, **25**(12):2683–2690.

Scarratt, D. J. (1973). Claw Loss and Other Wounds in Commercially Caught Lobsters

(*Homarus americanus*). *Journal of the Fisheries Research Board of Canada*, **30**(9):1370–1373.

Schauber, E. M., Storm, D. J., and Nielsen, C. K. (2007). Effects of Joint Space Use and Group Membership on Contact Rates Among White-Tailed Deer. *Journal of Wildlife Management*, **71**(1):155–163.

Schliehe-Diecks, S., Kappeler, P. M., and Langrock, R. (2012). On the application of mixed hidden Markov models to multiple behavioural time series. *Interface Focus*, **2**(2):180–189.

Scopel, D. A., Golet, W. J., and Watson III, W. H. (2009). Home range dynamics of the American lobster, *Homarus americanus*. *Marine and Freshwater Behaviour and Physiology*, **42**(1):63–80.

Scopel, D. A., Watson, W. H., Golet, W. J., and Cooper, A. B. (2006). Daily patterns of locomotion expressed by american lobsters (*Homarus americanus*) in their natural habitat. *Journal of Crustacean Biology*, **26**(4):610–620.

Scrivener, J. (1971). Agonistic behaviour of the American lobster *Homarus americanus* (Milne-Edwards) Fisheries Board of Canada Technical Report No.235.

Shears, N. T., Grace, R. V., Usmar, N. R., Kerr, V., and Babcock, R. C. (2006). Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. *Biological Conservation*, **132**(2):222–231.

Sheehy, M. R. J. and Bannister, R. C. A. (2002). Year-class detection reveals climatic modulation of settlement strength in the European lobster, *Homarus gammarus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**:1132–1143.

Shelton, R. G. J. (1981). How lobsters get into traps. *Scottish Fish. Bull.*, **46**:24–26.

Shepherd, S. A. and Clarkson, P. S. (2001). Diet, feeding behaviour, activity and predation of the temperate blue-throated wrasse, *Notolabrus tetricus*. *Marine and Freshwater Research*, **52**(3):311.

Shirabe, T. (2006). Correlation Analysis of Discrete Motions. In Raubal, M., Miller, H. J., Frank, A. U., and Goodchild, M. F., editors, *Geographic Information Science*, volume 4197 of *Lecture Notes in Computer Science*, pages 370–382. Springer Berlin Heidelberg, Berlin, Heidelberg.

Siddeek, M., Zheng, J., Punt, A., and Vanek, V. (2016). Estimation of size–transition matrices with and without molt probability for Alaska golden king crab using tag–recapture data. *Fisheries Research*, **180**:161–168.

Silverman, B. W. (1986). *Density Estimation for Statistics and Data Analysis*. Chapman and Hall, Boca Raton, Florida, USA.

Simpfendorfer, C. A., Heupel, M. R., and Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**(1):23–32.

Skajaa, K., Ferno, A., Lokkeborg, S., and Haugland, E. K. (1998). Basic movement pattern and chemo-oriented search towards baited pots in edible crab (*Cancer pagurus* L.). *Hydrobiologia*, **371/372**(165583):143–153.

Skerritt, D., Robertson, P., Mill, A., Polunin, N., and Fitzsimmons, C. (2015). Fine-scale movement, activity patterns and home-ranges of European lobster *Homarus gammarus*. *Marine Ecology Progress Series*, **536**:203–219.

Skerritt, D. J. (2014). *Abundance, interaction and movement in a European lobster stock*. PhD thesis, Newcastle Univeristy.

Skog, M. (2009a). Intersexual differences in European lobster (*Homarus gammarus*): recognition mechanisms and agonistic behaviours. *Behaviour*, **146**(8):1071–1091.

Skog, M. (2009b). Male but not female olfaction is crucial for intermolt mating in European lobsters (*Homarus gammarus* L.). *Chemical Senses*, **34**(2):159–169.

Skog, M., Chandrapavan, A., Hallberg, E., and Breithaupt, T. (2009). Maintenance of dominance is mediated by urinary chemical signals in male European lobsters, *Homarus gammarus*. *Marine and Freshwater Behaviour and Physiology*, **42**(2):119–133.

Smith, B. M. and Jamieson, G. S. (1989). A model for standardizing Dungeness crab (*Cancer magister*) catch rates among traps which experienced different soak times. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**(9):1600–1608.

Smith, G. W., Urquhart, G. G., MacLennan, D. N., and Sarno, B. (1998a). A comparison of theoretical estimates of the errors associated with ultrasonic tracking using a fixed hydrophone array and field measurements. *Hydrobiologia*, **372**(165481):9–17.

Smith, I. P., Collins, K. J., and Jensen, A. C. (1998b). Electromagnetic telemetry of lobster (*Homarus gammarus (L.)*) movements and activity: preliminary results. *Hydrobiologia*, **372**:133–141.

Smith, I. P., Collins, K. J., and Jensen, A. C. (1998c). Movement and activity patterns of the European lobster, *Homarus gammarus*, revealed by electromagnetic telemetry. *Marine Biology*, **132**(4):611–623.

Smith, I. P., Collins, K. J., and Jensen, A. C. (1999). Seasonal changes in the level and diel pattern of activity in the European lobster *Homarus gammarus*. *Marine Ecology Progress Series*, **186**:255–264.

Smith, I. P., Collins, K. J., and Jensen, A. C. (2000). Digital electromagnetic telemetry

system for studying behaviour of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology*, **247**:209–222.

Smith, I. P., Jensen, A. C., Collins, K. J., and Mattey, E. L. (2001). Movement of wild European lobsters *Homarus gammarus* in natural habitat. *Marine Ecology Progress Series*, **222**:177–186.

Smith, M. T. and Addison, J. T. (2003). Methods for stock assessment of crustacean fisheries. *Fisheries Research*, **65**(1-3):231–256.

Smith, S. J. and Tremblay, M. J. (2003). Fishery-independent trap surveys of lobsters (*Homarus americanus*): Design considerations. *Fisheries Research*, **62**(1):65–75.

Soetaert, K. and Meysman, F. (2012). Reactive transport in aquatic ecosystems: Rapid model prototyping in the open source software R. *Environmental Modelling and Software*, **32**:49–60.

Soetaert, K., Petzoldt, T., and Woodrow Setzer, R. (2010). Solving differential equations in R: package deSolve. *Journal of Statistical Software*, **33**(9):1–25.

Sosa-Cordero, E., Arce, A. M., Aguilar-Dávila, W., and Ramírez-González, A. (1998). Artificial shelters for spiny lobster *Panulirus argus* (Latreille): an evaluation of occupancy in different benthic habitats. *Journal of Experimental Marine Biology and Ecology*, **229**:1–18.

Stebbing, P., Johnson, P., Delahunty, A., Clark, P. F., McCollin, T., Hale, C., and Clark, S. (2012). Reports of American lobsters, *Homarus americanus* (H. Milne Edwards, 1837), in British waters. *BioInvasions Records*, **1**(1):17–23.

Stehfest, K. M., Lyle, J. M., and Semmens, J. M. (2015). The use of acoustic accelerometer tags to determine seasonal changes in activity and catchability of a recreationally caught marine teleost. *ICES Journal of Marine Science*, **72**(8):2512–2520.

Steneck, R. S. and Wilson, C. J. (2001). Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. *Marine and Freshwater Research*, **52**(8):1303–1319.

Stephenson, F., Mill, A. C., Scott, C. L., Stewart, G. B., Grainger, M. J., Polunin, N. V., and Fitzsimmons, C. (2018). Socio-economic, technological and environmental drivers of spatio-temporal changes in fishing pressure. *Marine Policy*, **88**(November 2017):189–203.

Stephenson, F., Polunin, N. V. C., Mill, A. C., Scott, C., Lightfoot, P., and Fitzsimmons, C. (2017). Spatial and temporal changes in pot-fishing effort and habitat use. *ICES Journal of Marine Science*, **74**(8):2201–2212.

Stewart, F. E. C., Fisher, J. T., Burton, A. C., and Volpe, J. P. (2018). Species occurrence

data reflect the magnitude of animal movements better than the proximity of animal space use. *Ecosphere*, **9**(2):e02112.

Stolwijk, A. M., Straatman, H., and Zielhuis, G. A. (1999). Studying seasonality by using sine and cosine functions in regression analysis. *Journal of Epidemiology and Community Health*, **53**(4):235–238.

Stoner, A. W. (2004). Effects of environmental variables on fish feeding ecology: Implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology*, **65**(6):1445–1471.

Svartberg, K. (2005). A comparison of behaviour in test and in everyday life: evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science*, **91**(1-2):103–128.

Swihart, R. K. and Slade, N. A. (1985). Testing for independence of observation in animal movements. *Ecology*, **66**(4):1176–1184.

Szuwalski, C. (2016). Biases in biomass estimates: The effect of bin width in size-structured stock assessment methods. *Fisheries Research*, **180**:169–176.

Tamm, G. R. and Cobb, S. J. (1978). Behavior and the crustacean molt cycle: changes in aggression of *Homarus americanus*. *Science*, **200**:79–80.

Taylor, E. W. (1982). Control and co-ordination of ventilation and circulation in crustaceans: responses to hypoxia and exercise. *Journal of Experimental Biology*, **100**:289–319.

Taylor, M. D., McPhan, L., van der Meulen, D. E., Gray, C. A., and Payne, N. L. (2013). Interactive Drivers of Activity in a Free-Ranging Estuarine Predator. *PLoS ONE*, **8**(11):e80962.

Therneau, T. M. (2015). A Package for Survival Analysis in S. version 2.38.

Thomas, H. J. (1955). Observations on the Sex Ratio and Mortality Rates in the Lobster (*Homarus vulgaris* Edw.). *ICES Journal of Marine Science*, **20**(3):295–305.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., and Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, **365**(1550):2163–2176.

Towner, A. V., Leos-Barajas, V., Langrock, R., Schick, R. S., Smale, M. J., Kaschke, T., Jewell, O. J. D., and Papastamatiou, Y. P. (2016). Sex-specific and individual preferences for hunting strategies in white sharks. *Functional Ecology*, **30**(8):1397–1407.

Tremblay, M. J. and Smith, S. J. (2001). Lobster (*Homarus americanus*) catchability in

different habitats in late spring and early fall. *Marine And Freshwater Research*, **52**:1551–1557.

Triantafyllidis, A., Apostolidis, A. P., Katsares, V., Kelly, E., Mercer, J., Hughes, M., Jørstad, K. E., Tsolou, A., Hynes, R., and Triantaphyllidis, C. (2005). Mitochondrial DNA variation in the European lobster (*Homarus gammarus*) throughout the range. *Marine Biology*, **146**(2):223–235.

Tully, O. (2001). Impact of the v-notch technical conservation measure on reproductive potential in a lobster (*Homarus gammarus* L.) fishery in Ireland. *Marine And Freshwater Research*, **52**:1551–1557.

Tuomainen, U. and Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, **86**(3):640–657.

Turchin, P. (1998). *Quantitative Analysis of Movement*. Sinauer Associates, Inc.

Turner, R. A., Gray, T., Polunin, N. V. C., and Stead, S. M. (2013). Territoriality as a Driver of Fishers' Spatial Behavior in the Northumberland Lobster Fishery. *Society & Natural Resources*, **26**(5):491–505.

Urbano, F., Cagnacci, F., Calenge, C., Dettki, H., Cameron, A., and Neteler, M. (2010). Wildlife tracking data management: a new vision. *Philosophical Transactions: Biological Sciences*, **365**(1550):2177–2185.

Vabø, R., Huse, G., Ferno, A., Jørgensen, T., Løkkeborg, S., and Skaret, G. (2004). Simulating search behaviour of fish towards bait. *ICES Journal of Marine Science*, **61**(7):1224–1232.

van de Kerk, M., Onorato, D. P., Criffield, M. A., Bolker, B. M., Augustine, B. C., McKinley, S. A., and Oli, M. K. (2015). Hidden semi-Markov models reveal multiphasic movement of the endangered Florida panther. *Journal of Animal Ecology*, **84**(2):576–585.

Van Der Meeren, G. I. . (1994). Sex- and Size-Dependent Mating Tactics in a Natural Population of Shore Crabs *Carcinus maenas*. *Journal of Animal Ecology*, **63**(2):307–314.

Van Der Meeren, G. I., Chandrapavan, A., and Breithaupt, T. (2008). Sexual and aggressive interactions in a mixed species group of lobsters *Homarus gammarus* and *H. americanus*. *Aquatic Biology*, **2**(June):191–200.

Van der Meeren, G. I., Ekeli, K. O., Jørstad, K. E., and Tveite, S. (2000). Americans on the wrong side – the lobster *Homarus americanus* captured in Norwegian waters. Technical Report U:20.

Van der Meeren, G. I. and Uksnøy, L. E. (2000). A comparison of claw morphology and dominance between wild and cultivated male European lobster. *Aquaculture International*, **8**(1):77–94.

Van Dyck, H. and Baguette, M. (2005). Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology*, **6**(6):535–545.

van Overveld, T. and Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, **6**(2):187–190.

Vannini, M. and Cannicci, S. (1995). Homing behaviour and possible cognitive maps in crustacean decapods. *Journal of Experimental Marine Biology and Ecology*, **193**(1-2):67–91.

Waddy, S. L. and Aiken, D. E. (1986). ization and Consecutive Spawning in Large American Lobsters,. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**:2291–224.

Wahle, R. A. (1992a). Body-size dependent anti-predator mechanisms of an American lobster. *Oikos*, **65**(May):52–60.

Wahle, R. A. (1992b). Substratum constraints on body size and the behavioural scope of shelter use in the American lobster . *J.Exp.Mar.Biol.*, **159**(1):59–75.

Wahle, R. A., Castro, K. M., Tully, O., and Cobb, J. S. (2013). Homarus. In Phillips, B. F., editor, *Lobsters: Biology, Management, Aquaculture and Fisheries*, chapter 8, pages 221–258. Wiley-Blackwell, 2nd edition.

Wahle, R. A. and Steneck, R. S. (1991). Recruitment habitats and nursery grounds of the American lobster *Homarus Americanus*: a demographic bottleneck? *Marine Ecology Progress Series*, **69**:231–243.

Wahle, R. A. and Steneck, R. S. (1992). Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology*, **157**(1):91–114.

Walden-Schreiner, C., Leung, Y.-F., Kuhn, T., and Newburger, T. (2018). Integrating direct observation and GPS tracking to monitor animal behavior for resource management. *Environmental Monitoring and Assessment*, **190**(2):75.

Walker, S. E., Marshall, S. D., Rypstra, A. L., and Taylor, D. H. (1999). The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). *Animal Behaviour*, **58**(3):515–520.

Walters, C. (2003). Folly and fantasy in the analysis of spatial catch rate data. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**(12):1433–1436.

Watkins, W. A. and Schevill, W. E. (1972). Sound source location by arrival-times on a non-rigid three-dimensional hydrophone array. *Deep Sea Research*, **19**(10):691–706.

Watson, W. and Jury, S. H. (2013). The relationship between American lobster catch, entry rate into traps and density. *Marine Biology Research*, **9**(1):59–68.

Watson III, W. H., Golet, W., Scopel, D., and Jury, S. (2009). Use of ultrasonic telemetry to determine the area of bait influence and trapping area of American lobster, *Homarus americanus*, traps. *New Zealand Journal of Marine and Freshwater Research*, **43**(1):411–418.

Watson III, W. H., Vetrovs, A., and Howell, W. H. (1999). Lobster movements in an estuary. *Marine Biology*, **134**(1):65–75.

Webster, D. and Weissburg, M. (2009). The Hydrodynamics of Chemical Cues Among Aquatic Organisms. *Annual Review of Fluid Mechanics*, **41**(1):73–90.

Webster, D. R. and Weissburg, M. J. (2001). Chemosensory guidance cues in a turbulent chemical odor plume. *Limnology and Oceanography*, **46**(5):1034–1047.

Wehkamp, S. and Fischer, P. (2013). The impact of coastal defence structures (tetrapods) on decapod crustaceans in the southern North Sea. *Marine Environmental Research*, **92**:52–60.

Weissburg, M. J. and Zimmer-Faust, R. K. (1993). Life and Death in Moving Fluids : Hydrodynamic Effects on Chemosensory-Mediated Predation. *Ecology*, **74**(5):1428–1443.

Whitehead, H. (2016). Consensus movements by groups of sperm whales. *Marine Mammal Science*, **32**(4):1402–1415.

Wiig, J. R., Moland, E., Haugen, T. O., and Olsen, E. M. (2013). Spatially structured interactions between lobsters and lobster fishers in a coastal habitat: fine-scale behaviour survival estimated from acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**:1468–1476.

Wilberg, M. J., Thorson, J. T., Linton, B. C., and Berkson, J. (2010). Incorporating Time-Varying Catchability into Population Dynamic Stock Assessment Models. *Reviews in Fisheries Science*, **18**(1):7–24.

Wilson, A. D. and Godin, J. G. J. (2009). Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology*, **20**(2):231–237.

Wilson, J. B. (1995). Null models for assembly rules: The Jack Homer effect is more insidious than the Narcissus effect. *Oikos*, **72**(1):139–144.

Wilson, R. P. and McMahon, C. R. (2006). A "missing" family of classical orthogonal polynomials. *Frontiers in Ecology and the Environment*, **4**(3):147–154.

Winner, K., Noonan, M. J., Fleming, C. H., Olson, K. A., Mueller, T., Sheldon, D., and Calabrese, J. M. (2018). Statistical inference for home range overlap. *Methods in Ecology and Evolution*, **9**(7):1679–1691.

Wolf, M., van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**:581–584.

Yackulic, C. B., Blake, S., Deem, S., Kock, M., and Uriarte, M. (2011). One size does not fit all: Flexible models are required to understand animal movement across scales. *Journal of Animal Ecology*, **80**(5):1088–1096.

Ye, Y. and Dennis, D. (2009). How reliable are the abundance indices derived from commercial catch–effort standardization? *Canadian Journal of Fisheries and Aquatic Sciences*, **66**(7):1169–1178.

Zeileis, A., Kleiber, C., and Jackman, S. (2008). Regression Models for Count Data in R. *Journal of Statistical Software*, **27**(8):1–25.

Zhang, J., O'Reilly, K. M., Perry, G. L. W., Taylor, G. A., and Dennis, T. E. (2015). Extending the Functionality of Behavioural Change-Point Analysis with k-Means Clustering: A Case Study with the Little Penguin (*Eudyptula minor*). *PLOS ONE*, **10**(4):e0122811.

Ziegler, P. E., Frusher, S. D., Johnson, C. R., and Gardner, C. (2002). Catchability of the southern rock lobster *Jasus edwardsii*. I. Effects of sex, season and catch history. *Marine and Freshwater Research*, **53**(8):1143–1148.

Zimmer-Faust, R. K. (1989). The relationship between chemoreception and foraging behavior in crustaceans. *Limnology and Oceanography*, **34**(7):1367–1374.

Zucchini, W., MacDonald, I. L., and Langrock, R. (2016). *Hidden Markov Models for Time Series: An Introduction Using R*. CRC Press, 2nd edition.

Zydelis, R., Lewison, R. L., Shaffer, S. A., Moore, J. E., Boustany, A. M., Roberts, J. J., Sims, M., Dunn, D. C., Best, B. D., Tremblay, Y., Kappes, M. A., Halpin, P. N., Costa, D. P., and Crowder, L. B. (2011). Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proceedings of the Royal Society B: Biological Sciences*, **278**(1722):3191–3200.

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Pepe the King Prawn